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Cultural Neuroscience

Cultural Influences on Brain Function

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JOAN CHIAO

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Preface

Cultural neuroscience is a new, interdisciplinary field bridging cultural psychology, neurosciences, and neurogenetics that seeks to explain how neurobiological processes, such as genetic expression and brain function, give rise to cultural values, practices, and beliefs as well as how culture shapes neurobiological processes across macro- and micro-time scales. Although the formal study of cultural neuroscience has only recently emerged in the past decade, the question of how culture and biology mutually constitute each other has long been a source of philosophical and scientific curiosity, dating as far back as the 7th century. Nevertheless, the theoretical and empirical tools necessary to make progress in these outstanding questions has only recently become available, providing an unprecedented opportunity for scientists to make novel discoveries concerning the universality and diversity in the dynamic interplay of genes, brain, and behavior.

There are several events over the past few years that have marked the arrival of cultural neuroscience as a rapidly growing field. First, notable cultural psychologists have demonstrated a growing interest in understanding how biology may give rise to cultural processes and vice versa by including the topic in the *Handbook of Cultural Psychology* and several symposia on cultural neuroscience at international cultural psychology meetings, such as Society for Personality and Social Psychology and American Psychological Society. A handful of smaller research workshop meetings held at Harvard University, University of Michigan, Hokkaido University, and Northwestern University between 2002 and 2009 also have played key roles in shaping the agenda for cultural neuroscience research. Cultural scientists trained in anthropology have showed similar interest by hosting a symposium on neuroanthropology at the American Anthropological Association meeting. Neuroscientists have also demonstrated increasing interest in incorporating cultural theory in the investigation of mind–brain mappings as demonstrated by strong attendance at symposia on cultural neuroscience at the international Organization of Human Brain Mapping meeting related presentations at the Cognitive Neuroscience Society meeting as well as inclusion of the topic in the *Handbook of Social Neuroscience*. Upcoming special issues in peer-reviewed journals such as *Social Cognitive and Affective Neuroscience* and *Asian Journal of Social Psychology* further demonstrate the growing global interest and viability of cultural neuroscience as a once and future discipline.

This volume of *Progress on Brain Research* represents the first collection of review articles on cultural neuroscience research presented in a comprehensive and integrated manner. As such, this volume signifies both the progress and the promise of this rapidly growing research area. Most of the reviews discuss evidence of culture-brain mappings, however, an important future frontier in cultural neuroscience is discovering how genetic variation at the population level may be associated with culture-brain mappings. An additional frontier for cultural neuroscience research is the incorporation of anthropological methods, such as experimentation within the field setting, to further determine how culture and biology interact on multiple time scales. Ultimately, the goal of the current volume is to provide a thorough overview of the current conceptual landscape as well as to reveal the important knowledge gaps in cultural neuroscience that will require a new generation of truly broad, interdisciplinary researchers dedicated to understanding dynamic culture–biology interactions to answer.

Finally, I would like to extend warm gratitude to invaluable colleagues, students, and friends who have generously shared their minds and enthusiasm with me and special thanks to my family for their unending encouragement and patience throughout.

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Contents

Section I. Conceptual Foundations of Cultural Neuroscience

Section II. Cultural Neuroscience of Attention and Perception

Section III. Cultural Neuroscience of Cognition

Section IV. Cultural Neuroscience of Social Cognition

Section V. Cultural Neuroscience of Emotion and Well Being

Section VI. Applications of Cultural Neuroscience

Section VII. Conclusion

SECTION I

Conceptual Foundations of Cultural Neuroscience

J.Y. Chiao (Ed.)
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CHAPTER 1

Controlled studies of chimpanzee cultural transmission

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Abstract: Following the first long-term field studies of chimpanzees in the 1960s, researchers began to suspect that chimpanzees from different African populations varied in their behavior, and that some of these variations were transmitted through social learning, thus suggesting culture. Additional reports of chimpanzee culture have since accumulated, which involve an increasing amount of behavioral variation that has no obvious ecological or genetic explanation. To date, close to 50 cultural variants have been reported, including subsistence behavior, tool-use, communication signals, and grooming patterns. Nevertheless, field studies lack the experimental controls and manipulations necessary to conclusively demonstrate that the observed variation results from differential invention and social transmission of behavior. This would require that behavioral variants have been learned from others, a question best addressed in a controlled experimental setting. The following chapter details a series of experimental studies at Yerkes National Primate Research Center of Emory University. In each case, the behavior of two captive groups (each $N = 12$ individuals) was compared before and after the introduction of a novel foraging behavior by a trained conspecific "inventor." The studies were designed to investigate (i) the conditions under which chimpanzees learn from one another, (ii) how behaviors are transmitted, (iii) how cultures are maintained over generations. The results emphasize the importance of integrating both fieldwork and experimental approaches. Previous studies have reported deficits in chimpanzees' cultural capacities, but did so after testing them with human models, which are largely irrelevant to the problem at hand. A representative understanding of culture can only be gained when efforts are made to create a naturalistic learning environment in which chimpanzees have opportunities to learn spontaneously from conspecifics in a familiar social setting.

Keywords: evolution; culture; learning; chimpanzee; human

Introduction

Culture is often viewed as a uniquely human capacity that separates us from other animals. Indeed, many contemporary definitions of culture exclude other species a priori, such as culture is "distinctly human" (Kottak, 2004, p. G5); or "The arts and other manifestations of human intellectual achievement regarded collectively" (Oxford English Dictionary, 2008). However, we can only make an assessment of the uniqueness of our own abilities by comparing them in a scientifically meaningful way with the abilities of other species.

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In this chapter, we discuss some of the controversies surrounding the concept of nonhuman culture and review recent studies of chimpanzee cultural behavior, which shed light on the evolutionary origins of our own cultures.

Nonhuman culture

The idea that nonhumans might share our ability for culture was first proposed over half a century ago by Japanese anthropologist Kinji Imanishi. He theorized that if the individuals within a species were able to learn from one another, then over time the behavior of distinct groups might begin to differ, eventually resulting in unique cultural variations (Imanishi, 1952). This definition implies that culture results from *learned* differences in behavior, importantly distinguishing cultural differences from differences in behavior owing to genetic or ecological variation. Nevertheless, the possibility of nonhuman culture has not always been well received. Some critics have suggested that learned behavioral differences in nonhumans are analogous rather than homologous to the human version. Thus, the word Culture (with a capital) should be reserved for humans, while the behavior of other species should be described as culture, or pre-culture (Menzel, 1973). But such semantic distinctions are hard to justify from an evolutionary perspective. Like all other species, humans are a product of natural selection, which has shaped the evolution of our behavior, including our cultural abilities. Hence, culture falls squarely within biology, and differentiating "Culture" from "culture" makes as little sense as claiming that humans have Respiration while other species have pseudo-respiration (de Waal, 2001; McGrew, 2004; de Waal and Bonnie, 2009). The definition of respiration is the same within biology, regardless of whether gas exchange takes place across the surface of lungs, gills, or skill. Culture, too, is best defined by its effects and functions rather than by a narrow set of underlying processes assumed to be unique to our species, such as language or active teaching. In recent years, several functional definitions of culture have been proposed, each echoing the central theme of Imanisji's original hypothesis: the function of culture is to pass behaviors to members of a group via learning. Cultural differences result when these behaviors vary among groups, either due to differential invention in each group or due to gradual changes in behavior over time. In order to identify culture, it must therefore be shown that these differences are not the result of genetic variation between groups, or differential expression of behavior due to habitat and ecology (Laland and Hoppitt, 2003).

With these functional definitions in hand, reports of culture have accumulated for species including monkeys (e.g., Perry et al., 2003); apes (e.g., Whiten et al., 1999; Hohmann and Fruth, 2003; van Schaik et al., 2003), rodents (e.g., Aisner and Terkel, 1992), fish (e.g., Bshary et al., 2002), birds (e.g., Madden, 2008), and marine mammals (e.g., Noad et al., 2000). Among these studies, reports of chimpanzee culture have received the greatest attention. This is due in part to the great number and diversity of chimpanzee cultural traditions in comparison to other species as well as their shared evolutionary history with humans.

Chimpanzee culture

Field studies of chimpanzee behavior date back to the 1960s when Jane Goodall set-up the first long-term study-site in Tanzania, East Africa. She spent many years habituating the chimpanzees so that she could closely follow and record their natural behavior. One of Goodall's main discoveries was that chimpanzees use tools in the wild, and that they modify tools for optimal use. Tool-making was previously assumed to be a unique and defining feature of humanity, as in Oakley's (1949) book "Man the Tool-Maker." The manufacture and use of tools was so fundamental to contemporary views of human culture that anthropologist Louis Leakey famously wrote "Now we must redefine tool, redefine Man, or accept chimpanzees as humans." Our unique status within the animal kingdom continued to be challenged as additional chimpanzee research sites were set up throughout Africa and reports of increasingly complex behavior accumulated.

Over time, it became apparent that there were differences in the behavior of chimpanzees at different sites, and that some of these differences might be cultural inasmuch as they did not have obvious alternative explanations. The pattern of behavior at each site was highly distinctive, a classic feature of human culture (Goodall, 1973; McGrew, 1992). The possibility of chimpanzee culture gained additional traction in 1999 following the publication of a large-scale comparison of behavior from seven sites in Africa (Whiten et al., 1999). Researchers from each site pooled their data to compile a list of all behavioral differences. Differences that had an obvious ecological explanation were excluded, such as ground nesting which differed between sites in relation to the presence or absence of predation by leopards (Whiten et al., 1999). Through this process of exclusion, the original list was whittled down to 39 behaviors that had no obvious alternative explanation. These included variants of courtship, grooming and tool-use, a diversity of variation previously undocumented in any other species.

Although the report generated considerable interest, critics were quick to point out that under the natural and uncontrolled conditions of fieldwork it is difficult to conclusively rule out ecological explanations for all 39 behaviors (Galef, 2003; Laland and Janik, 2006). For example, habitats that seem indistinguishable to the human observer could still be sufficiently different so as to provide determinants of behavioral expression in chimpanzees. These concerns have been addressed in part by a small number of highly innovative studies, some observational and some experimental.

Excluding noncultural explanations

McGrew et al. (1997) investigated the potential influence of ecology on the distribution of nut-cracking behavior among West African chimpanzee populations. Nut cracking is one of chimpanzees' most sophisticated tool-use behaviors as it involves the combination of two separate tools (a hammer and anvil) and temporal and spatial bimanual coordination to successfully crack open hard shelled nuts (Hayashi et al., 2005).

The authors systematically compared the availability of nuts and appropriate stone or wooden tools at several sites, revealing that there was no obvious ecological explanation for the observed distribution of behavior. Chimpanzees at sites where nut cracking was absent had all the appropriate raw materials to perform the behavior and did not have alternative high-energy food sources that would preclude the need to eat nuts. The authors concluded that the absence of nut cracking at these sites was cultural, insofar as the behavior had not been invented and therefore had not spread to become part of the groups' cultural repertoire (McGrew et al., 1997).

The influence of ecology has also been addressed by a series of natural experiments. The chimpanzees of Bossou, Guinea, crack oil palm nuts (*Elaeis guineensis*) with stone tools as part of their normal foraging behavior. Matsuzawa and colleagues (1994) set-up an ‘‘outdoor laboratory’’ on a small hilltop frequently visited by the Bossou chimpanzees. They provided a novel species of coula nut (*Coula eduris*) found at a neighboring site but not at Bossou. An adult female, who had most likely immigrated into the Bossou community from the neighboring group appeared to be familiar with the new nuts and after a short time started to crack them. She was closely observed by several members of the Bossou group and soon the new variant of behavior began to spread, strongly suggesting transmission via observation and social learning (Matsuzawa, 1994).

Finally, a recent study by Lycett et al. (2007) set out to address the role of genetic variation in the expression of chimpanzee behavior. The authors used cladistic analysis of the behaviors reported by Whiten et al. (1999), to determine whether the distribution of behavior was correlated with the genetic distribution of four chimpanzee subspecies. They concluded that there was no significant relationship between genetics and behavior and therefore the behavioral variants performed by wild chimpanzees are best explained by differential invention and subsequent transmission via social learning, consistent with culture.

While these innovative studies go some way to excluding noncultural explanations, they do not conclusively demonstrate that learning underpins the spread of behavior, as it is extremely difficult to see ‘‘learning-in-action’’ in the field: only the final product of learning and the resulting intergroup variation can be accurately recorded.

Several studies conducted in captivity have filled this gap. Although the potential contribution of captive studies is high, they have typically failed to accurately simulate the complex social and environmental conditions under which learning occurs in the wild. Previous studies have often investigated how chimpanzees learn from a human in a dyadic learning environment, whereby the chimpanzee is physically separated from the human, preventing close observation and typical social interaction. Many of these studies are conducted from a comparative perspective to determine whether chimpanzees acquire cultural behavior in the same way as human children, and have been criticized for inadvertently favoring human participants while posing handicaps for the apes (de Waal, 2001; Boesch, 2007; de Waal et al., 2008). For example, in contrast to chimpanzees, children are typically tested without physical separation, in close proximity to a parent, and by a member of their own species. Whereas the relatively poor performance of chimpanzees in such studies has been used to argue that they are incapable of learning with the accuracy required for cultural transmission (Richerson and Boyd, 2005), the conditions under which learning is assessed make these results of limited relevance to the question of culture. It seems more likely that chimpanzees will demonstrate learning that is representative of their natural abilities with conspecific models.

In the following section, we present two studies designed specifically to create a learning environment more representative of that which chimpanzees might experience in the wild, while also maintaining the controlled experimental conditions afforded by a captive setting. The objective of the studies was (i) to determine if cultural behaviors could be initiated in captivity, and (ii) to investigate how cultures spread within a group and are sustained over time.

Initiating culture in captivity

Like human culture, chimpanzee cultures likely arise when new behaviors are introduced to a population either by immigrating individuals (Matsuzawa and Yamakoshi, 1998), or through invention within an existing group (Goodall, 1986; McGrew, 2004). These new behaviors are then transmitted within the group through social learning. In each of the studies below, we set out to simulate invention of new behavior by training one chimpanzee model from each of two large social groups (both groups $n = 17$) to use an alternative, yet equally difficult behavior to gain food from the same apparatus. By seeding each group with a different variant of the behavior, we could determine if, and how, each variant spread to potentially become cultural.

The identity of the original "inventor" was therefore critically important. Theoretical models predict that members of a group should be choosey about who they learn from (Boyd and Richerson, 1985; Laland, 2004) with several factors such as skill competence, rank and social tolerance directly influencing the likelihood that the actions of an individual will be copied (Coussi-Korbel and Fragaszy, 1995; Boesch and Tomasello, 1998). Of these factors, social tolerance between a performer and potential learners is thought to be particularly important because it (i) allows close observation of behavior, (ii) creates a relaxed social atmosphere which encourages attention to the task without the threat of aggression, and (iii) allows proficient individuals to perform without fear of being displaced (van Schaik et al., 1999; van Schaik, 2003). Additionally, reports from the wild indicate that chimpanzees tend to learn complex foraging skills from older or similar aged female social models (Goodall, 1986; Biro et al., 2003; Lonsdorf et al., 2004). On this basis, we reviewed observational data recording the social relationships among group members collected during previous years and picked two high-ranking, socially tolerant adult female models: Georgia in group 1 and Ericka in group 2.

Study 1: social transmission within a group

In this first experiment, we trained Georgia and Ericka to each use a different method to retrieve grapes from a device called the "panpipe."

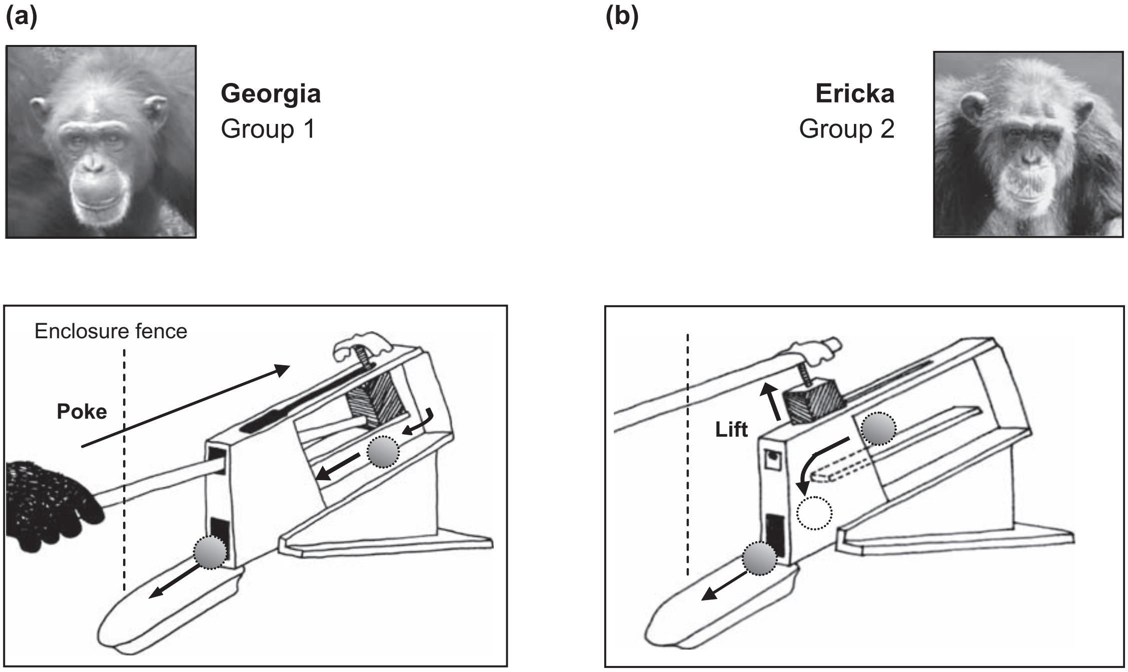

Fig. 1. Panpipe apparatus: (a) model Georgia from group 1 was trained to exclusively use the poke method to retrieve food from the panpipe; (b) model Ericka from group 2 was trained to exclusively use the lift method. Both methods were always possible. Adapted from Whiten et al. (2005).

The panpipe gets its name because chimpanzees use a stick to release grapes trapped behind a block inside a large pipe (see Fig. 1; Whiten et al., 2005). In group 1, Georgia was trained to poke the block backwards so that the grape rolled off the top ledge and down toward her waiting hand (see Fig. 1a). Meanwhile in the group 2, Ericka was trained to use the same tool to lift the block out of the way so that the grape rolled down the pipe toward her (see Fig. 1b). By having a different "inventor" in each group, we could determine how the alternative methods might spread. The behavior of each group was compared to six chimpanzees in a control group who were not given opportunities to observe a trained model, but were allowed to explore the panpipe apparatus and potentially discover a solution by trial and error.

We found that the alternative methods spread differentially within each group, such that the chimpanzees in group 1 who observed Georgia use the poke method almost exclusively use poke, and chimpanzees in group 2 who observed Ericka use lift, used lift significantly more than the alternative (Whiten et al., 2005). The six chimpanzees from the control group failed to discover either solution.

Moreover, when we retested each group two months later, we found that the small number of chimpanzees in group 2 who had used the alternative method to some degree in the original study, had shifted their preference toward the lift method used by Ericka and the majority of their groupmates (see Fig. 2). This finding suggests a type of conformity, defined in anthropology as the tendency for members of a group to discount personal experience in favor of the behavior most commonly performed by others (Henrich and Boyd, 1998). Boyd and Richerson (1985) propose that in human culture, conforming to the majority behavior conveys a selective advantage by increasing the probability that conformers will adopt behaviors that are adaptive for their environment. The conformity indicated in this study strongly implies that similar learning biases

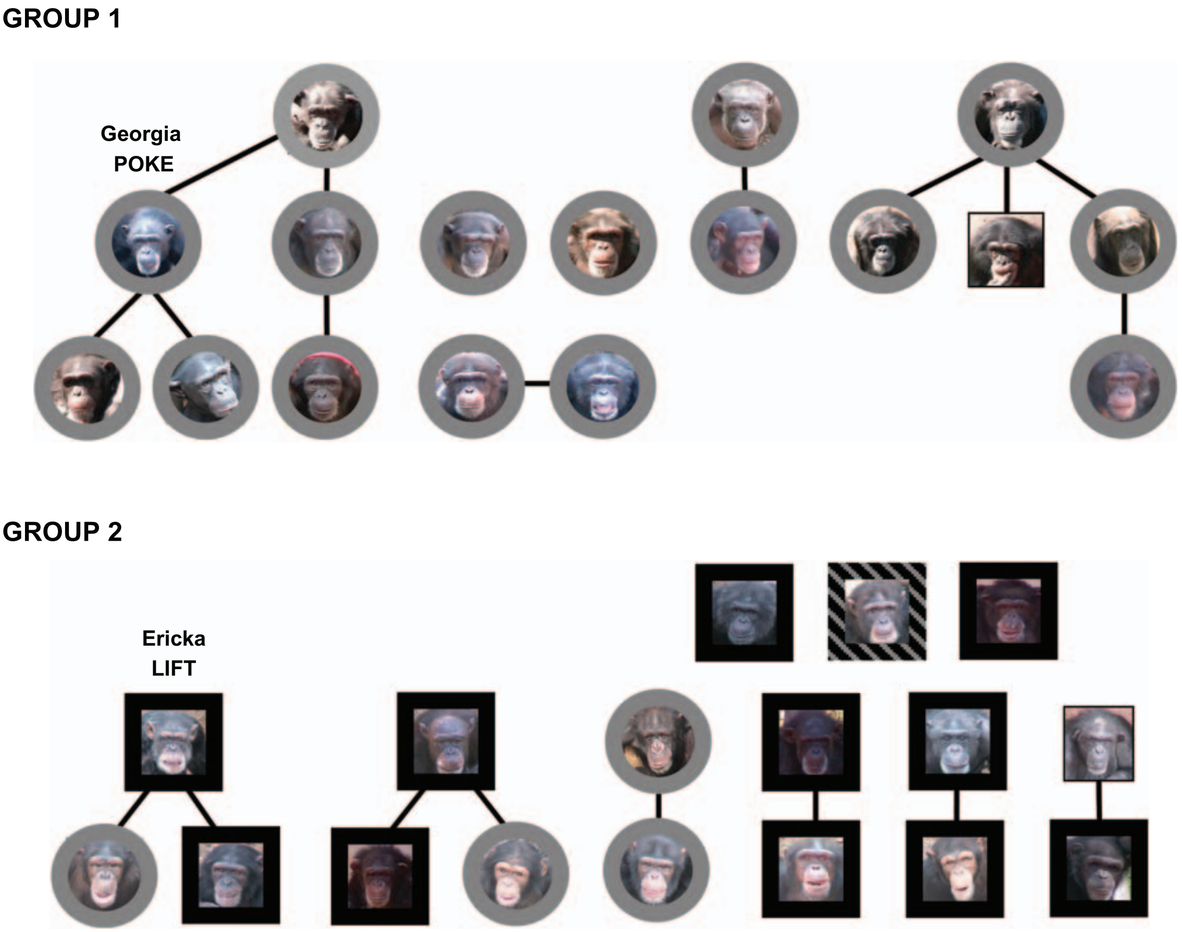

Fig. 2. Schematic of family tree relationships among chimpanzees from groups 1 and 2. The figure shows the trained models in each group and the preferred method used by each chimpanzee to retrieve food from the panpipe when retested 2 months after the initial study. If an individual did not participate in the retest, the figure shows their preference in the initial study. Gray circles indicate chimpanzees who used poke on the majority of trials, while black squares indicate a preference for lift. Gray and black stripes indicate an equal preference for both lift and poke.

may operate in chimpanzees, and may have deeper evolutionary roots that previously expected (Whiten et al., 2005).

This study also demonstrates that chimpanzees have the ability to accurately learn from one another in a manner that can lead to behavioral differences between groups. The role of social learning is further supported by the poor performance of the control group, which did not have an opportunity to watch a skilled performer. This study thus supports the assertion that the group-typical behavior patterns of wild chimpanzees result from differential invention and transmission of behavior.

The importance of social tolerance

We believe that the successful, differential transmission of behavior was greatly influenced by the natural learning environment that we exploited and the high degree of social tolerance exhibited by the chimpanzees. Both Georgia and Ericka were able to retain control of the Panpipe apparatus during the initial phase of the study, despite being observed by up to 10 groupmates closely packed around them. Although some scrounging was seen, they were both able to keep the majority of food that they retrieved. The first observer to succeed in each group was a high-ranking adult male (group 1 — Socrates, α-male; group 2 — Amos, β-male). Yet, despite the high rank of these individuals, they continued to tolerate close observation by the rest of their group, a characteristic that distinguishes chimpanzee (as well as human and bonobo males) from the males of other ape species (Russon, 2003; van Schaik, 2003). In addition, we witnessed 106 instances of coaction involving 38 different chimpanzee pairs, only 7 of which occurred between kin. Coaction occurs when a performer allows observers to participate intimately in their behavior (Visalberghi and Fragaszy, 1990). This was seen when a chimpanzee who was using the panpipe allowed an observer to either touch their hand or part of the tool as they worked. Although some limited scrounging was seen in this study, it was not observed during bouts of coaction, where models kept 100% of their food rewards. In the wild, chimpanzees likely gain useful information about skills such as tool-use by observation, and through being involved in the ongoing actions of conspecifics. For example, nut cracking is learned by young chimpanzees over a period of many years through a process of apprenticeship (Matsuzawa, 2001). During this time infants have opportunities to interact with unused hammers and anvils and broken nut-shells as well engage in coaction with tolerant adult performers, possibly gaining valuable physical and visual information about successful execution of behavior. The results of this study indicate that, like human culture, social tolerance may be a key component of culture in chimpanzees.

The role of rewards

In this study, the chimpanzees were directly rewarded for performing a successful behavior, and so the motivation to learn is rather obvious. However, this is not always the case. As discussed above, it takes infants in the wild many years to learn to proficiently crack nuts, during which time their attempts are unsuccessful (Matsuzawa, 1994). Their perseverance is not reinforced by physical rewards, but instead may be motivated by the intrinsic reward of copying others, particularly those with whom they have a positive social relationship (de Waal, 2001; Matsuzawa, 2001). The underlying motivation to copy others is a fundamental aspect of human behavior and can easily be seen when watching children at play. However, it has often been overlooked in studies of learning in other species. The importance of social rewards was investigated in a recent study with capuchin monkeys, in which observers were given opportunities to copy the behavior of a trained conspecific under three conditions; both monkeys were rewarded, only the model was rewarded, or neither monkey was rewarded (Bonnie and de Waal, 2007). The authors found that observers were motivated to copy the actions of the model, even when neither monkey received a tangible physical reward. Social rewards should therefore also be acknowledged as an important motivator in chimpanzee learning.

Who learned from whom?

It was not possible to accurately determine who learned from whom because several chimpanzees typically watched each performer working on the task. While it is possible that all successful performers learned from the original trained models, it is also possible that they were influenced by observing each chimpanzee who solved the task before them. From a cultural perspective this is a more interesting possibility as it indicates the ability to pass behavior from one chimpanzee to the next in a chain-like fashion. Chain transmission would, theoretically, enable behaviors to be passed between chimpanzees from different generations and therefore sustain culture for extended periods. This is of particular interest in light of a recent report indicating that certain chimpanzee populations in West Africa have been using stone tools to crack nuts for several thousand years (Mercader et al., 2007). The authors used archeological techniques to date the strata in which the tools were found to approximately 4300 years old.

On the other hand, if the chimpanzees in our study learned only from the original trained "inventor" the cultural differences that we observed would eventually die out with the original learners as the behavior could not be passed on. This would draw into question the idea that chimpanzees can sustain cultural behavior over many generations. Chain transmission was therefore the subject of our second study.

Study 2: sustainability of cultural behavior

In order to explore chimpanzees' capacity for chain transmission we explored a second type of paradigm called a "diffusion chain" to determine if and how behavior might degrade or corrupt as it is passed between successive chimpanzees in a chain. Diffusion chains were first employed to study human memory by exploring how narrative stories altered as they were passed from one person to the next (Bartlett, 1932). Single chains were later used in a small number of nonhuman studies to investigate habituation to novel stimuli in chimpanzees (Menzel et al., 1972), predator avoidance in birds (Curio et al., 1978), food preferences and foraging in rats (Laland and Plotkin, 1993), and foraging pathways in fish (Laland and Williams, 1998).

In a diffusion chain paradigm only one observer is allowed to watch the initial trained model before being given an opportunity to solve the task themselves. If the observer successfully solves the task (irrespective of the method used), they then become the model for a third individual, and so forth down the chain. This methodology is more tightly controlled than the previous study because individuals are added to each chain one by one. Nevertheless, it has several advantages because the identity of both the model and observer are known during each link in the chain, making it possible to determine when, and infer why, breakdowns in transmission might occur.

Running each chain in a manner likely to simulate a naturalistic learning environment is complex because in order to be representative of chimpanzees' learning abilities, the chain must respect the normal social dynamics of the group, with many factors such as rank, affiliation, and social tolerance influencing who is more likely to learn from whom. We based the order of chimpanzees in each chain on the order in which the chimpanzees had succeeded in the previous panpipe study, as a rough measure of social tolerance. Changes to the predetermined order were made only if there were known social incompatibilities between certain pairs based on our weekly observations of each group.

The apparatus was a rectangular box that contained grapes concealed behind a hidden door on the front panel (see Fig. 3a; Horner et al., 2006). In order to retrieve the grapes, the door could either be lifted open on a hinge, or slid sideways to the right on a spring-loaded track (see Fig. 3c and d). Like the previous study, both methods were judged to be equally difficult and were equally effective in retrieving the grapes.

The models from the previous study were trained using the same positive reinforcement procedure to perform one of the two alternative techniques (group 1, Georgia — lift; group 2, Ericka — slide). In each group, the trained model was observed by the next chimpanzee in the chain. If the second chimpanzee was successful in opening the door using either technique, he/she became a model for the third chimpanzee in the chain, and so forth. The same apparatus was also given to six chimpanzees from the control group. Three control participants failed to discover the door at all, two discovered the lift door technique and one discovered slide indicating that the task was difficult, but that both techniques could be discovered by trial and error.

Progressing down the chains we were able to build two chains involving five and six transmissions, respectively. All chimpanzees performed the same technique as the original model in their group: the only variation occurred in group 2 when Barbie (BB) performed one lift, possibly accidentally, which was not transmitted further. Each chain had some side branches were pairings had to be changed due to incompatible social dynamics, or successful chimpanzees did not wish to participate as models for the next individual in the chain (see Fig. 4). These breakdowns in transmission were highly informative. In the group 2 chain, Vivienne (VV) failed to learn a

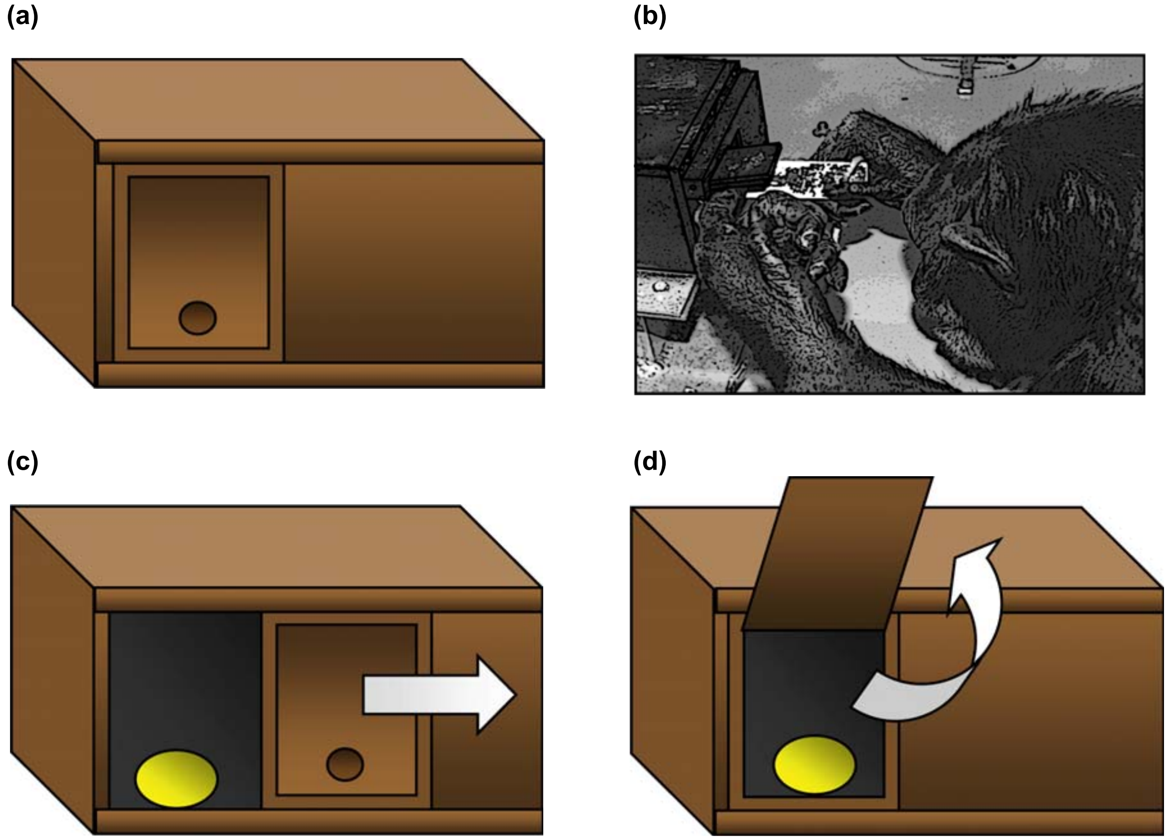

Fig. 3. Diffusion chain apparatus: (a) the starting position with door closed, (b) lift door method, (c) slide door method, and (d) outlined photograph of model Georgia performing the lift method at the start of the diffusion chain in group 1. Adapted from Horner et al. (2006).

solution when paired with Cynthia (CY), but learned successfully when re-paired with Ericka, indicating a lack of social tolerance rather than a deficit in social learning. This observation lends support to the Bonding and Identification-based Observational Learning model (de Waal, 2001), in which learning must be preceded by a desire to act like the model, as evidenced by Vivienne's apparent motivation to learn from Ericka, but not Cynthia. This illustrates the importance of distinguishing *motivational* issues from *cognitive* abilities, particularly when interpreting the failure of individuals to learn in a dyadic social learning experiment (de Waal, 2001). Individuals may completely fail to acquire novel behaviors, or fail to learn accurately because a lack of social tolerance inhibits their ability to gain the necessary visual and social information required to solve the task, or because they are simply not motivated to learn from the model. This possibility should be taken into account when interpreting negative data in dyadic laboratory studies of chimpanzee cognition.

Correspondingly, in the wild tolerance of younger individuals by adults appears to play an important role the acquisition of tool-use skills such as honey dipping (Hirata and Celli, 2003), termite fishing (Lonsdorf, 2006), and nut cracking as well as the development of cooperative foraging in bonobos and hunting in chimpanzees (Hare et al., 2007).

Since the order of each chain was predetermined, breakdowns in transmission resulted in dead-end "side branches" and "kinks" in the main chain. However, in a more naturalistic environment, such as Study 1, it is possible that

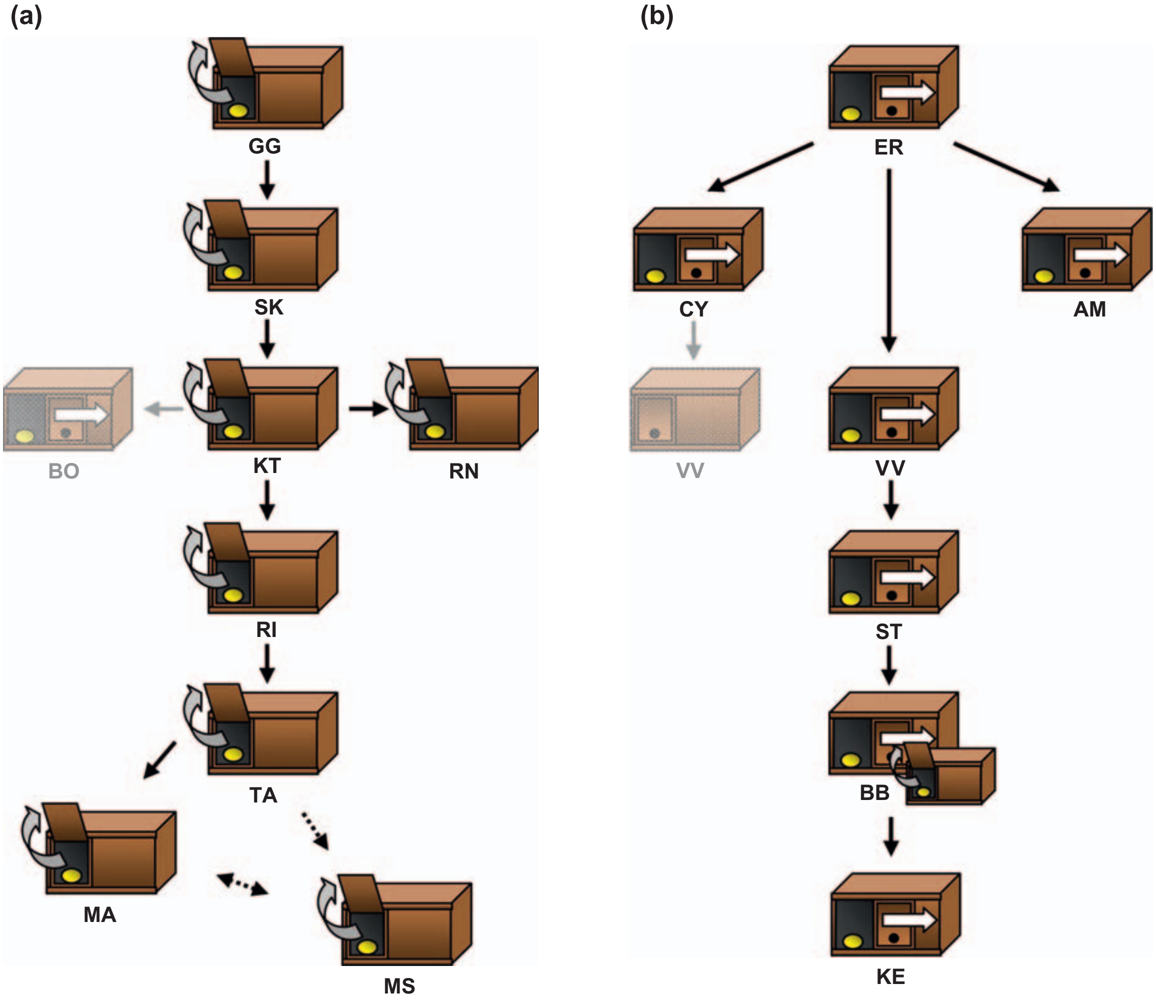

Fig. 4. Schematic representation of the diffusion chains in (a) group 1 and (b) group 2. Each chain was initiated by a trained model (group 1, Georgia — lift; group 2, Ericka — slide). The method used by each chimpanzee is indicated by a gray arrow (lift) or a white arrow (slide). ID codes of each chimpanzee are in bold (see Table 1). Side branches represent chimpanzees who successfully opened the box, but declined to participate as models for the next individual in the chain. Borie (BO) and Vivienne (VV) did not observe the behavior of the model they were paired with. Tara (TA) demonstrated for Mai (MA) and Missy (MS) at the same time because they are a mother–daughter pair and only volunteer to participate in studies if they are together. Reinette (RN) and Amos (AM) successfully learned from Georgia and Ericka respectively, but declined to participate as models.

these side branches might become side chains. Thus, social *intolerance* between individuals may act to fracture or split lines of transmission, resulting in complex transmission patterns in the wild (Horner et al., 2006).

The chains terminated in each group when there were no further volunteers, but with more participants it is possible that the chains might have been much longer. Nevertheless, a chain composed of six transmission events between mothers and daughters in the wild would hypothetically correspond to about 80 years, much longer than any existing field site. This finding lends support to the hypothesis that many chimpanzee cultures reported in the wild may be very old (cf. nut cracking, Mercader et al., 2007), and substantially predate the first scientific observations of the behavior.

Table 1. ID codes for chimpanzees from FS1 and FS2 who participated in the diffusion chain study of cultural transmission

FS1				FS2			
Name	ID	Sex	Birth year	Name	ID	Sex	Birth year
Georgia	GG	F	1980	Ericka	ER	F	1973
Socko	SK	M	1987	Cynthia	CY	F	1980
Katie	KT	F	1989	Vivienne	VV	F	1974
Reinette	RN	F	1987	Amos	AM	M	1981
Borie	BO	F	1964	Steward	ST	M	1993
Rita	RI	F	1987	Barbie	BB	F	1976
Tara	TA	F	1995	Kerri	KE	F	1995
Mai	MA	F	1964				
Missy	MS	F	1993				

Conclusion

Technology has now advanced to the point were we are able to conduct sophisticated studies of the neurological underpinnings of human culture, such as those discussed in the following chapters. But a comprehensive understanding of culture must also take an evolutionary approach comparing our abilities to those of other animals in a scientifically meaningful way.

The studies presented in this chapter are supportive of the view that the geographic patterning of behavior found in wild chimpanzees represents cultural variation. Moreover, chimpanzee and human culture share many features, such as conformity and a reliance on social tolerance, indicating that these aspects of human culture may have deeper evolutionary roots than previously thought.

These studies also demonstrate that social transmission can be simulated and studied under controlled experimental conditions to provide insights into the cultural minds of chimpanzees. However, this can only be informative if care is taken to respect the social structure of the group, acknowledge differing levels of social tolerance between participants and understand the importance of social and physical interaction in a naturalistic learning environment. If these criteria are carefully considered, captive studies can provide an informative compliment to observational studies of wild chimpanzee behavior, and when combined together are likely to build the most representative picture of chimpanzee cultural minds. Only then can we begin to better understand the evolution of or own cultural abilities.

Acknowledgments

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CHAPTER 2

Brain in macro experiential context: biocultural co-construction of lifespan neurocognitive development

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Abstract: For more than a century, neuroscientists have recognized that the brain is an open, adaptive system and that the organism's experiences are environmentally contextualized. However, the proposition that socio-cultural contexts may exert reciprocal influences on neurobiological mechanisms is rarely considered and could not be empirically explored until very recently. This article reviews the emerging trend of interdisciplinary research aiming at exploring the effects of socio-cultural influences on human brain functioning. Recent co-constructive views of brain development and functioning and empirical evidence of developmental plasticity at different levels are reviewed. Empirical findings that are indicative of reciprocal influences of social contexts, culture-specific language environment, and expertise training are highlighted. The quest to understand how individual brains get personalized through lifespan development that takes place in the macro socio-cultural experiential context is still at an embryonic stage. Nevertheless, studies reviewed here indicate that new conceptual and empirical opportunities for this endeavor are emerging.

Keywords: brain plasticity; situated brain; neuromodulation; cognitive development; cognitive aging

Introduction

> Mental exercise facilitates a greater development of …the nervous collaterals in the part of the brain in use. In this way, preexisting connections between groups of cells could be reinforced…
>
> Cajal (1894), Croonian lecture to the Royal Society (cited in Squire and Kandel, 1999, p. 35).

As the foregoing quote from Ramón y Cajal's (1894) Croonian lecture to the Royal Society indicates, for over a century neuroscientists have been interested not only in how neural mechanisms implement mental experiences, but also in how experiences may exert reciprocal influences on the neurobiological substrates of behavior and mental processes. Indeed, since Ramón y Cajal first enunciated what today is known as the "activity-dependent synaptic plasticity and memory hypothesis" (Martin et al., 2000) and the

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formulation (Hebb, 1949) and discoveries (Bliss and Lømo, 1973; Kandel and Tauc, 1964; Wigström and Gustafsson, 1981) of synaptic processes of memory and learning, a great variety of neurochemical singling mechanisms involved in tuning the efficacy of synaptic connections have been identified (see Bliss et al., 2003 for review).

As Rosenzweig (1996) gathered in his seminal review, animal research conducted in the second half of the 20th century showed that differential experience (or training) provided by environmental contexts with varying levels of complexity could alter brain neurochemistry, anatomy, and electrophysiology to varying degrees, indicating brain plasticity at these various levels. The research on the functional effects of these various aspects of brain plasticity on behavior and cognition are well underway and are being applied in studies of different variants of neural plasticity during development (e.g., Greenough and Black, 1992) and aging (Meaney et al., 1991; Mohammed et al., 1993). Furthermore, aside from the predominant emphasis of experiential influences on neuronal and synaptic plasticity, recent studies have also started to investigate the effects of experience on non-neuronal changes, such as experience-induced plasticity of astrocytes, myelination, and cerebrovasculature. In summary, current evidence indicates that, in response to different types (or aspects) of experiences (e.g., activity, learning, or task demands) the brain exhibits multiple forms of plasticity, allowing its processes at different levels to adapt to various forms of experiential tunings (see Grossman et al., 2002 for review).

From complex environment paradigm in animal research to macro socio-culturally constructed experiential contexts in humans

Since the complex environment housing paradigm was developed in the late 1940s and early 1950s by Hebb (1949) and his associates (Forgays and Forgays, 1952; Hymovitch, 1952) and first used as a method for studying neural plasticity by Bennett et al. (1964) in the mid-1960s, research on neural plasticity has recognized that the brain is an open, adaptive system (Grossman et al., 2002) and that the organism's experiences are contextualized in the environmental contexts they take place. Rarely considered, however, is the proposition that socio-cultural contexts may also exert reciprocal influences on neurobiological mechanisms. Understandably, hitherto such a proposition has been atypical for neuroscientists to consider empirically, if not conceptually. Lacking techniques for studying brain functioning in vivo in humans during most of the last century, the relevance of social, and particularly, cultural contexts for animal studies is not only minimum but also hard to define. Therefore, the research has, instead, been considering the effects of empirically more tractable aspects of environment, such as the relative complexity and space of the animal's home cage, or simple proxies of social interactions, such as group size or amount of handling (see Reuter-Lorenz et al., 2000 for review).

One could also argue that experience *is* the proximal channel through which the influences of external contexts are mediated (Nelson, 1999); hence, it may be more practical to consider experience-dependent neural plasticity, instead of contemplating on influences from macro contexts, such as socio-culturally constructed experiential contexts. Indeed, contextual influences interact with neurobiological processes through the organism's behavioral and cognitive experiences. However, environmental complexity simulated in laboratories is typically below the level of complexity in natural settings. This is particularly true for research on human brain functioning, given that human behavioral, emotional, and cognitive experiences are embedded in socio-culturally constructed experiential contexts whose complexity and diversity are way beyond the proxies of environmental complexity and social interaction animal studies have considered. Furthermore, in humans, cultural resources that have, thus far, accumulated through cumulative cultural evolution (Tomasello, 1999) and the ongoing social dynamics in contemporary societies structure the modal experiences the individuals go through in different life periods (Cole, 1999). For instance, socio-culturally based knowledge, such as the knowledge of language and numerical systems are learned by individuals through parent–child interaction and from formal schooling. Basic skills of reading, writing, computing, and professional skills, as well as other expertises are also acquired and exercised through different life periods in socio-culturally constructed contexts.

Moreover, there are great socio-cultural diversities in contemporary societies, which give rise to a wide range of differential experiences for individuals developing, going through adult life, and aging in these divergent experiential contexts (Hart and Risley, 1995; Kitayama, 2000; Montgomery et al., 2003; Stern and Carstensen, 2000). With the arrival of a range of neuroimaging techniques to study human brain functioning, it has now become possible to explore the influences of socio-cultural contexts on brain plasticity at different levels.

This brief, selective review focuses on a recently emerging trend of interdisciplinary research that starts to explore socio-cultural influences on brain development and functioning across the lifespan. The article begins with a brief overview of recent co-constructive views of brain development and functioning and evidence of developmental plasticity at the evolutionary, behavioral and cognitive, neural, and genetic levels. Findings showing neural plasticity across different life periods are then highlighted. While only limited evidence is available, three selective sets of recent findings are reviewed to demonstrate the influences of social context, culture-specific language environment, and expertise trainings on brain functioning. In the concluding section, some potentially fruitful future research directions are considered.

Co-constructive views of brain development and functioning

> The brain's capacity to produce and combine mental objects, to remember them, and to communicate them is seen most vividly in humans. *Mental representations are propagated in different coded forms from one individual to another and perpetuate themselves through generations, without requiring any sort of genetic mutation…*
>
> Writing leaves an impression on the brain, but where? Our lack of knowledge here does not allow us much room for speculation. We might expect that many areas are involved… But neurological data are often hard to interpret; moreover, experimentation is difficult, if not impossible. Nevertheless, *the diversity of human culture provides fantastically rich material…* (J.-P. Changeux, 1985, pp. 241, 244; *italicization* added).

Co-constructivism (or related interactionism) per se is not new. Conceptions of environmental, cultural, and behavioral factors interacting with the biological inheritance of human development have long philosophical traditions. For instance, at the level of individual ontogeny, in the late 18th century Tetens (1777) assigned extraordinary plasticity to human nature, thus stipulating opportunities for environmental, cultural, and individual regulation during lifespan development. At the evolutionary phylogenetic level, in the late 19th century St. George Jackson Mivart (1871) suggested that behavioral changes and adaptation precede and affect natural selection. Modern behavioral researchers of human development have also been sensitive to the interplay between biology and various aspects of developmental contexts. Conceptually, there is the consensus that individual ontogeny is hierarchically organized within an open developmental system with multiple levels of contexts, from micro to macro. Developmental phenomena, thus, need to be investigated by jointly considering the reciprocal interactions between endogenous (e.g., genetic and neurobiological) and exogenous (socio-cultural and environmental) processes at various levels (Baltes, 1979; Bronfenbrenner, 1979; Bronfenbrenner and Ceci, 1994; Gottlieb, 1976, 1998; Magnusson, 1988; Piaget, 1954). Advocating the necessity and benefits of integrating socio-cultural influences into neurobiological research also does not only stem from the viewpoint of behavioral researchers. In the field of neurobiology, as expressed in the quote above, Jean-Pierre Changeux (1985) saw the possibility of “cultural imprint” (p. 241) and stressed the importance of integrating cultural influences into neuroscience research nearly 20 years ago.

Developmental plasticity at different levels and recent co-constructive views

> … Recent work in neuroscience, robotics, and psychology… stresses the unexpected intimacy of brain, body, and world and invites us to attend to the structure and dynamics of extended adaptive systems… While it needs to be handled with some caution, I believe there is much to be learned from this broader vision. *The mind itself, if such a vision is correct, is best understood as the activity of an essentially situated brain: a brain at home in its proper bodily, cultural, and environmental niche.* (A. Clark, 2001, p. 257; *italicization* added).

However, more active interdisciplinary theoretical and empirical endeavors aim at investigating the influences of socio-culturally constructed experiential contexts on brain development and functioning did not begin until very recently. The above quote by Clark (2001) and a recent symposium on brain, mind, and culture participated by neuroscientists, cognitive neuroscientists, cognitive and developmental psychologists (Baltes et al., 2006) are good examples of an emerging trend of interdisciplinary research that seeks to understand brain development and functioning as adaptations to broader experiential contexts. Contrary to the nativist view of innate and encapsulated genetic and neurobiological processes, across various subfields of life and developmental sciences there is a clear reemerging Zeitgeist of co-constructive conceptions that are accompanied by much recent empirical support for developmental plasticity at different levels. These conceptions and evidence of developmental plasticity across various levels have been integrated in a recent metatheoretical framework of development that advocates brain and cognitive development be considered as continual biocultural co-construction of neurocognitive representations across the lifespan (Li, 2003). As schematically shown in Fig. 1, an integral whole of biocultural influences on lifespan brain and behavioral development is implemented through reciprocal interactive processes and developmental plasticity that are simultaneously embedded within three time scales (i.e., phylogenetic, ontogenetic, and microgenetic times) encompassing multiple levels (i.e., socio-cultural, behavioral, cognitive, neurobiological, and

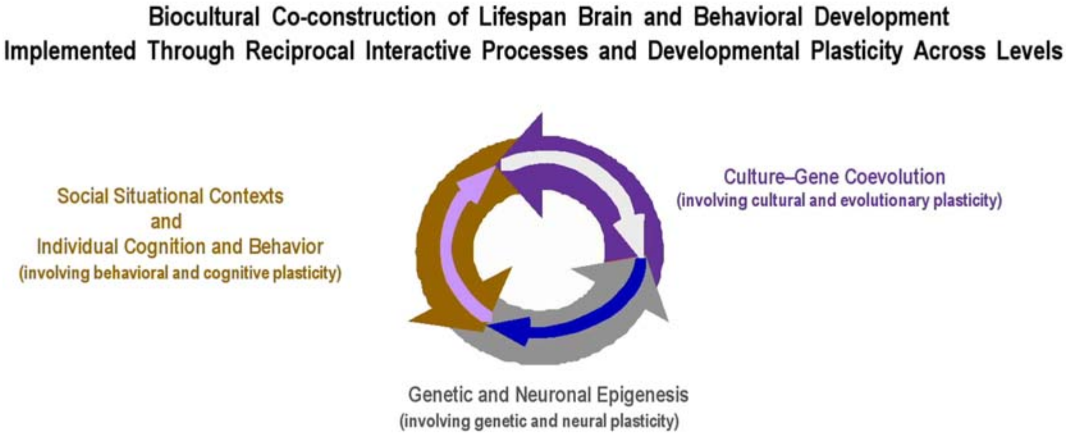

Fig. 1. Schematic diagram of the cross-level dynamic biocultural co-constructive framework of development, showing that concerted biocultural influences are implemented through interconnected interactive processes and developmental plasticity across various levels. Adapted with permission from Li (2003).

genetic). Individual ontogeny throughout life is seen as a dynamic process that is cumulatively traced out by moment-to-moment experiences and activities taking place through interactions across the behavioral, cognitive, and neurobiological levels on the microgenetic time scale. These moment-to-moment microgenetic events are couched within (a) the proximal developmental context involving culturally embedded social interactions and situations on the lifespan ontogenetic time scale and (b) the distal context of culture-gene coevolution occurring on the long-term phylogenetic time scale. In the following, co-constructive notions and evidence of developmental plasticity at the various levels are reviewed.

Evolutionary plasticity

Recently, it has been argued both on empirical and theoretical grounds that genetic programs and brain organizations reflect the socio-cultural basis of evolution. The conventional coevolutionary theory has been extended by postulating a set of mediating mechanisms called ''niche construction'' to relate biological evolution and cultural changes to each other (Laland et al., 2000). Central to the concept of niche construction is the capacity of organisms and individuals to modify and construct the sources of natural selection in their environment via (a) learning and experience-dependent processes during individual ontogeny and (b) processes of cultural change on another scale. For instance, the dairy farming culture selects for adult lactose tolerance and leads to populations in dairy farming societies with a higher percentage (i.e., over 90%) of lactose absorbers in comparison to the percentage of lactose absorbers (i.e., below 20%) in societies without dairy faming (Aoki, 1986; Feldman and Cavalli-Sforza, 1989). Consider a different example regarding brain evolution, Dunbar (1993) proposed that the biological evolution of brain encephalization was, in part, driven by the increase of social group size and the emergence of language as a more efficient means for handling complex social interactions.

Behavioral and cognitive plasticity

As for developmental plasticity at the behavior and cognitive levels, various theories in the field of developmental psychology have emphasized the malleability of behavior and cognition by contextualized experiential factors (see Collins et al., 2000; Lerner, 1998, for reviews). For instance, Vygotsky (1978) had already emphasized the role of social interactions in proximal developmental contexts, such as parent–child relation, peer relation, and schooling in promoting an individual's attained level of development toward a higher level of potential. More recently, sociocultural contextual approaches (e.g., Cole, 1999; Gauvain, 1995) have focused more specifically on cultural influences affecting these social interactions and their subsequent mediated effects on individual development. In a related but different vein, rather than focusing on cultural influences at a higher level, the relationship contextual approach (e.g., Reis et al., 2000) examines fine-grained details (e.g., emotional and cognitive aspects) of different types of interpersonal relationships and their impact on child development. Still, others focus on the linguistic environment as a main facet of culture-specific social interactions in an individual's proximal developmental context (Nelson, 1996). Cross-culture studies on parenting style (Bornstein et al., 1991) found that differential emphases on interpersonal versus object orientation that were mediated through parent–child interactions in the Japanese and American cultures, respectively, affected the types of games and languages at which the toddlers in these two societies performed well. It has also been suggested that the differential emphases of holistic versus analytical thinking in the East Asian and Western cultures, respectively, are associated with individuals' causal–attribution processes (Nisbett et al., 2001). As for cognitive plasticity across the lifespan, memory-training studies showed that older adults (aged 60–80) still displayed a fair amount of cognitive plasticity in improving their memory performance after training (Baltes and Kliegl, 1992), and that in very old age (i.e., age 80 years and above) marginal cognitive plasticity is still preserved (Singer et al., 2003).

Although memory plasticity is to a large extent still preserved in old age, older adults do show more limited plasticity not only in comparison to younger adults, but also to children and teenagers (Brehmer et al., 2007).

Neural plasticity

Shifting to the neuronal level of analysis, building on evidence showing experiential influences on synaptic numbers, axonal arborization, and dendritic arborization as well as neurocomputational studies exploring learning and activity-dependent representational complexity, Quartz and Sejnowski (1997) proposed "*neural constructivism*" to consider representational features of the synaptic connections as built from dynamic interactions between neural growth mechanisms, on the one hand, and environmentally derived neural activity. On a related theme but at the level of cortical functional specification during development, unlike most previous studies focusing primarily on intrinsic factors (e.g., the expressions of molecular markers) on cortical specialization, Kingsbury et al. (2002) recently advocate that cortical specialization, particularly, specification involving later layers of the cortical plate (e.g., layers IV, II/III) are results of interactions between intrinsic factors and extrinsic input (e.g., somatosensory thalamic input). Similarly, in order to emphasize that brain development and functioning are co-constructed by contextualized experiences and neural processes, instead of speaking about "experience-dependent" neural plasticity, some researchers now prefer the term "experience-induced," which more clearly indicate the active, constructivist role of experiential contexts (e.g., Greenough and Black, 1992; Grossman et al., 2002; Nelson, 1999, 2000).

Genetic plasticity

Regarding developmental plasticity at the genetic level, there is a recent shift from the traditional view of unidirectional gene → protein information flow (Crick, 1958) to a probabilistic-epigenetic framework emphasizing bi-directional interactions among genes, neuronal activity, behavior, and environment (Gottlieb, 1998). At this level, behavior-initiated evolutionary change also highlights that behaviors play active roles, instead of simply being the outcomes determined by genetic processes. For instance, it has been suggested that behavioral changes incurred during development could instigate genetic changes if transgenerational rearing conditions were relatively stable (Gottlieb, 2002).

Brain plasticity across the lifespan

One important but less emphasized aspect of the evidence on plasticity is that neural plasticity occurs even after maturation, beyond infancy and early childhood (see also Nelson, 1996 for review). Regarding plasticity during early development, accumulating data suggest that the functional specialization of the neocortex is established through subsequent epigenetic interactions with the immediate experiential context (Changeux, 1985; Johnson, 2001; O'Leary, 1996). Thus, experiential influences leave traces in developing brains capturing cumulative developmental effects accumulated through the individual's moment-to-moment activities and experiences. For instance, recently it has been demonstrated that face processing is less localized or specialized (i.e., not as differentiated) in infants than in adults. In infants, face processing involves both left and right ventral visual pathways, whereas in adults face processing primarily involves the right ventral visual pathway. While adult brain activity shows specific sensitivity to upright human faces, no such sensitivity for face orientation is observed in young infants (de Haan et al., 2002a, b).

Regarding plasticity after maturation, there is also increasing evidence for cortical and cognitive plasticity extending beyond the developing brain to other periods of the lifespan (see review in Li, 2003). Many recent data show that the adult brain can also adaptively change its structural and functional organization in response to accumulated developmental history reflecting daily experiences and aging. For instance, Maguire et al. (2000) found that the brain region involved in storing spatial representation of the environment (i.e., posterior hippocampi) of adults who had extensive navigation experience was significantly larger in comparison to age controls. As for functional plasticity during aging, a series of recent neuroimaging data found evidence for reorganization of cortical functions in old age. In comparison to the more clearly lateralized cortical information processing in young adults, people in their 60 s and beyond showed bilateralized (bi-hemispheric) activity during memory retrieval (e.g., Cabeza, 2002; Cabeza et al., 1997) and during both verbal and spatial working memory processing (e.g., Reuter-Lorenz, 2002; Reuter-Lorenz et al., 2000). It has been suggested that these data might indicate that the aging brain could "recruit" cortical areas in both hemispheres to compensate for neurocognitive declines during aging.

As for structural plasticity in old age, recently neuroscience's century-old dogma that there is no addition of new neurons in the adult mammalian brain has also been revised. There is now evidence showing that increased environmental complexity stimulates the growth of new hippocampal neurons (i.e., neurogenesis) in the adult brains of various species, such as birds, rats, and humans (see Gross, 2000 for review). There are also recent data showing that physical exercise training that increases aerobic fitness reduces aging-related loss in gray and white matter density (Colcombe et al., 2003).

Furthermore, recent evidence indicates that neurotransmitter systems may also be sensitive to training. This opens a new level for considering brain plasticity, namely in terms of neurochemical plasticity. Specifically, working memory training, which improves working memory capacity, is associated with changes in the density of cortical dopamine D1 receptors both in the prefrontal and parietal regions (McNab et al., 2009). Various aspects of the dopaminergic system (e.g., pre-synaptic, post-synaptic, and related enzyme activities) are known to decline during aging (see Bäckman et al., 2006 for recent review). A potential sequence of effect from deficient dopaminergic modulation in the aging brain leading to greater neuronal processing noise and less distinctive neuronal representations of perceptual and memory stimuli with ensuring consequences on more limited memory plasticity was demonstrated in a neuromodulation of cognitive aging theory close to a decade ago (Li et al., 2001; Li, 2002; Li and Lindenberger, 1999, 2002). The new findings (McNab et al., 2009) showing that the dopaminergic system is sensitive to memory training suggest that cognitive interventions for enhancing cognitive functions in old age may have a clear neurochemical root.

In summary, socio-cultural influences could have effects on the brain's structural and functional organization through early experiential "tuning" of synaptic connections and functional circuitry. In addition, though less flexible than in the early part of development, there is still marked cortical plasticity throughout most of the adult lifespan, both in terms of structural and functional plasticity. This opens up possibilities for cultural and experiential influences to be intimately integrated into the individual's cumulative developmental history reflecting lifelong adaptations to both ongoing life experiences couched in the respective socio-cultural context and lifespan developmental change in the efficacy and integrity of the brain itself.

Initial evidence of biocultural co-construction of neurocognitive functioning

As the interdisciplinary research on biocultural co-construction of lifespan neurocognitive development is still in a very early developing stage, available studies are limited. Nevertheless, three sets of selective findings reviewed in this section demonstrate, particularly, the reciprocal influences of social contexts, culture-specific language environment, and expertise training.

Coevolution of language, social group size, and brain encephalization

Focusing predominantly on the human phylogenetic scale, Dunbar (1993) showed that group size covaries with relative neocortical volume in nonhuman primates. This led to the proposal that the brain's encephalization is not driven by the cognitive demands of tool making, but by an intricate coevolving process between the growth in social group size and the development of language as a more efficient method for social bonding. More recent data comparing the complexity of social structure in New World and Old World monkeys, in part, also supported this proposal. Clark et al. (2001) found that the neocortical volume of Old World monkeys as well as some orders of New World monkeys with more complex social structure resembling that of Old World Monkeys is larger than New World monkeys with less complex social structure. The subsequent effect on the level of individual ontogeny, in turn, was for language to become part of the socially inherited species-specific cultural resources for different societies to support the individuals' interactions with each other and with the environment. Indeed, the linguistic relativity theory (Saunders and van Brakel, 1997; Whorf, 1956) contends that human understanding of the world is, in part, constructed through language.

Brain encephalization is also correlated with the extended juvenile period in primates and humans, possibly also arising from social selection pressures involved in managing complex and dynamic social environments (Bjorklund and Pellegrini, 2000; Joffe, 1997). The extended juvenile period in humans, in turn, allows an extended amount of time and opportunities for intergenerational social interactions, operating in conjunction with language and other cultural resources, to influence brain and cognitive development.

Culture-specific language environment and cortical language processing

Culture-specific language differences do not only affect language processing at the perceptual and cognitive levels. Recent findings indicate a dynamic shift in cortical organization over the course of language acquisition (see Neville and Bavelier, 1998 for review). For instance, the time-course of the changes and the degree of experience-dependent changes vary with different aspects of language. Event-related potentials (ERP) data indicated that at 20 months, when children are typically speaking in single-word utterances, open-class words (i.e., words conveying referential meaning) and closed-class words (i.e., words provide structural and grammatical information) elicit similar patterns of brain activity. At 28–30 months of age, when children typically begin to speak in short phrases, ERPs to open- and closed-class words reveal different patterns of brain activity. By 3 years of age when most children speak in sentences and use closed-class words appropriately like adults, ERPs start to display a left hemisphere asymmetry similar to adults (Neville and Mills, 1997). In a related vein, neuroimaging data indicate strong left hemisphere activation for the native language in bilinguals. While early bilinguals (second language learned before 7 years of age) showed overlapping areas of cortical activation for native and second language (Kim et al., 1997; Whorf, 1956), late bilinguals showed completely independent or less overlapping activation (Neville and Bavelier, 1998; Neville et al., 1998).

Although language processing depends on a system of neural networks primarily in the left hemisphere, within the common system, however, there is room for the progressive developmental history of learning and using languages differing in their orthographical mapping complexity to leave its trace at the cortical level. In comparison to the Italian language, English orthography is rather inconsistent, with complicated mappings of letters to sounds. In the English language there are over 1000 ways of representing 40 sounds (phonemes), whereas in the Italian language 33 graphemes are sufficient to represent 25 phonemes. Paulesu et al. (2000) recently found that Italian readers showed greater activation in the left superior temporal regions associated with phoneme processing, whereas English readers showed greater activations, particularly for non-words, in the left posterior inferior temporal gyrus and anterior frontal gyrus, areas associated with word retrieval during both reading and naming tasks. These data seem to suggest that acquiring the rather complex orthographical mapping of the English language impels the English readers to invoke additional neurocognitive mechanisms involving word retrieval from semantic memory while reading.

In addition, other culture, society-based symbolic tools could also affect cognitive processing.

At the neurobiological level, there is evidence for dissociated digit and letter processing with the area of left inferior occipitotemporal cortex responding significantly more during a letter than during a digit-recognition task. Interestingly, one recent study showed that even a rather non-salient aspect of cultural practice, that is, what the postal codes are composed of, affects the individual's letter and digit processing (Polk and Farah, 1998). In comparison to their fellow postal workers who do not sort mail, mail sorters who daily sort outgoing mails to Canada shows less behavioral evidence for segregated letter and digit processing, as the Canadian postal codes are a mixture of both digits and letters (e.g., V6K 2E8). An intriguing question is whether the behavioral findings observed in this case can also be found at the level of cortical processing.

Expertise and training-induced neural plasticity

Besides language, there is also evidence showing that acquiring other expertise such as music or navigation skills leads to experience-induced cortical functional reorganization. It was found that cortical representations of the fingers of the left playing hands of string players were larger than those of the right hand holding the bow, and this was particularly true for individuals who started playing the instrument early in life (Elbert, 2003). Another more recent neuroimaging study compared expert musicians with nonmusicians and found that while listening to J. S. Bach's *Italian Concerto*, nonmusicians who were not familiar with classical music showed activity primarily in the secondary auditory association area in the right temporal cortex. The musicians, however, also showed activities in the auditory association area in the left temporal cortex and in the left posterior dorsolateral prefrontal cortex, the brain regions associated with language processing and working memory functions, respectively (Ohnishi et al., 2001).

Outside the domain of music, Maguire et al. (2000) found that given their extensive navigation experience, London taxi drivers' posterior hippocampi, a region of the brain involved in storing spatial representation of the environment, were significantly larger in comparison to same-aged individuals who did not have as much navigation experience. Furthermore, when comparing among drivers, the number of years spent as a taxi driver correlated positively with hippocampal volume. These data indicate that the adult brain still possesses functional plasticity allowing the posterior hippocampus to expand regionally in order to accommodate elaboration of environmental spatial representation in individuals who rely heavily on their navigation skills and have achieved a high level of navigation expertise in a particular environment.

Future research directions and conclusion

Currently, findings regarding socio-cultural influences on lifespan neurocognitive development are still very limited and leave many gaps between the different levels of analyses. Nevertheless, the fact that there are emerging co-constructive views and empirical evidence of developmental plasticity at various levels as reviewed in this article indicate that, at least, the possibilities for bridging these gaps are gradually rising. Given neural plasticity that responds to lifespan developmental changes in the integrity of the brain itself as well as lifelong adaptations to ongoing life experiences couched in the individual's own respective socio-cultural context, future research will need to focus less on the commonly used localization approach to study neurocognitive processes mainly by analyzing regional activation differences as a function of task conditions. Instead, lifespan changes and individual differences in brain-behavior mapping need to be considered more explicitly (Li and Lindenberger, 2002). For instance, instead of assuming that cortical regions and circuitry associated with particular functionalities in normal adult are very similar, if not identical, to those in developing children or old adults, lifespan changes in brain-behavior mapping need to be investigated and taken into account (Cabeza, 2002; Grady et al., 2003; Karmiloff-Smith, 1998; Reuter-Lorenz, 2002; Schlaggar et al., 2002; Thomas and Karmiloff-Smith, 2002). Moreover, with the advent of genomic imaging approaches

(Harriri and Weinberger, 2003), the questions of how genetic-based individual differences may interact with contextual influences (e.g., aging, environmental support in the form of medication or cognitive training for instance) to affect cognitive (e.g., Nagel et al., 2008) and brain (Mattay et al., 2003) functions can now be directly examined.

Furthermore, given the highly interactive nature of neurocognitive processes involving constant information exchanges with the experiential contexts, future research needs to more explicitly consider information exchanges between the individual and the context, and how such interactions may affect the functional aspects of neurocognitive processing. For instance, in addition to studying neural substrates of social cognition (Adolphs, 2001), how dynamic, on-line social interactions may affect functional circuitry involved in different aspects of social cognition could also be of interest.

So far, we have only focused on findings showing adaptive neural plasticity induced by supportive socio-cultural contexts. However, as Nelson (1999) pointed out, plasticity can be a two-edged sword. Thus, at the applied level, the maladaptive effects of neural plasticity couched in changing societies where subjective social isolation (loneliness) increases for individuals of all ages (Cacioppo et al., 2003) or dysfunctional social contexts that cause individuals highly stressful experiences or even trauma (Nelson, 2000; Elbert et al., 1995) also need to be investigated. In addition, applied research on providing technological supports to assist individuals with limited neurocognitive capacity to better maintain the flow of information exchange between them and their experiential contexts is also important.

In conclusion, together the existing empirical evidence of developmental plasticity at different levels presents a warning against the "pure reductionist approach" to the genetic and neuronal bases of mind and behavior that ignores the influences from cultural, experiential, and cumulative developmental contexts. The reason is clear: genetic activities and neural mechanisms themselves possess remarkable plasticity awaiting socio-cultural contexts to exert reciprocal influences on them and to be the "co-authors" of mind and behavior. People are more than mere biological organisms; human mind and behavior need to be understood by situating them properly within a brain in a body that lives in an eventful world abounding with objects and people. Indeed, the brain offers the necessary biophysical reality for individual cognition and action; it alone, however, is not sufficient to engender the mind or behavior. On the mind-brain continuum, the individual mind is the expression emerging from the personalized brain (Greenfield, 2000; Llinas and Churchland, 1996). The very processes for personalizing the biological faculty of the mind take place throughout lifespan development in environmental and socio-cultural contexts, which entail intimate dynamical exchanges between nature and nurture.

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CHAPTER 3

Anthropology and cultural neuroscience: creating productive intersections in parallel fields

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Abstract: Partly due to the failure of anthropology to productively engage the fields of psychology and neuroscience, investigations in cultural neuroscience have occurred largely without the active involvement of anthropologists or anthropological theory. Dramatic advances in the tools and findings of social neuroscience have emerged in parallel with significant advances in anthropology that connect social and political-economic processes with fine-grained descriptions of individual experience and behavior. We describe four domains of inquiry that follow from these recent developments, and provide suggestions for intersections between anthropological tools — such as social theory, ethnography, and quantitative modeling of cultural models — and cultural neuroscience. These domains are: the sociocultural construction of emotion, status and dominance, the embodiment of social information, and the dual social and biological nature of ritual. Anthropology can help locate unique or interesting populations and phenomena for cultural neuroscience research. Anthropological tools can also help "drill down" to investigate key socialization processes accountable for cross-group differences. Furthermore, anthropological research points at meaningful underlying complexity in assumed relationships between social forces and biological outcomes. Finally, ethnographic knowledge of cultural content can aid with the development of ecologically relevant stimuli for use in experimental protocols.

Keywords: culture; social hierarchy; embodiment; emotion; ritual

Introduction

Anthropology has traditionally considered itself the expert discipline when it comes to generating insights about the workings of culture. However, much anthropological research on sociocultural systems and their consequences has not emphasized quantitative analysis or hypothesis testing. As a result, anthropological insights about the role of culture in behavior and biology have been difficult to integrate into experimental and biological studies.

Perhaps partially due to this oversight, anthropology's assumed monopoly on culture knowledge has been recently challenged. Other fields (from public health to neuroscience) have moved forward in studying cultural variation and processes, largely without the formal input of anthropologists. This push forward has coincided with the proliferation of new technologies that are adept at peering into the inner biological workings of humans, including the workings of the brain.

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The results of research on variation in assumed human universals using such technologies have been rich and fascinating.

It is now incumbent upon the field of anthropology to make culture knowledge accessible to other scientific fields, including the emerging field of cultural neuroscience. To help enable a collaborative endeavor between anthropology and cultural neuroscience, we describe five domains of inquiry in which anthropological knowledge could be particularly informative to the field: the sociocultural construction of emotion; the study of power, dominance, and hierarchy; the embodiment of social knowledge; and ritual. Throughout, we suggest research topics and strategies that would capitalize on the generative potential of intersections between cultural neuroscience and anthropology.

Sociocultural construction of emotion

Anthropological approaches to emotion have tended to emphasize the cultural specificity of emotion across different populations (Lutz, 1982; Mead, 1953). Generally, this work takes the position that emotions should always be studied in local cultural context, via long-term ethnographic work in which the researcher lives in the community long enough to familiarize herself with the diverse settings that elicit emotional response, comes to learn local emotion terms, and so forth. The message of this work is that research which focuses on universal aspects of emotion — including comparative work across cultural settings — runs the risk of missing fundamentally social-contextual nature of emotion generation, perception, and expression.

This position has generally been at odds with the work of Ekman and Oster (1979), who have identified elements of emotion that appear to be human universals. Via decades of research in the laboratory and in ethnographic field settings (such as Papua New Guinea), this research has discovered remarkable cross-cultural overlap in the underlying facial anatomy of “fundamental” emotions (e.g., fear, anger) as well as the broad aspects of social context in which such emotions are generally elicited. Within psychology, there are ongoing debates about the universality versus cultural specificity of emotion. Among other topics, these debates focus on the coherence (or lack thereof) of biological, behavioral, and subjective levels of analysis, and whether a dimensional approach to emotion (approach–avoidance, pleasure–displeasure, arousal level, etc.) might better describe variability in emotional response than specific emotion terms (Barrett et al., 2007; Russell, 2003).

As with many epistemological dichotomies, the answer lies somewhere in between the “strong” version of relativistic and universalistic approaches to emotion. However, the proper resolution space is not a weakened version of both propositions at once (in the same way that “behavior is 50% genes, 50% environment” is not a satisfactory resolution of the false dichotomy between “nature” and “nurture”). One key advantage of anthropological work is that it shows how cultural systems find their way into almost every aspect of experience and socialization throughout the life course. Culture helps to entrain and regulate emotion at the same time that emotion provides the mechanisms by which sociocultural systems constitute and reproduce themselves.

We will now provide several examples of how culture and emotion are intimately interwoven, focusing on ways in which these points of intersection could generate new research projects or directions in cultural neuroscience. Perhaps the most heavily cited evidence for cultural variation in emotion is the existence of emotion terms that appear to be culturally specific. For example, in Japan, *amae* refers to the desire to be socially dependent on others, an emotion word that does not have a direct English analog (Markus and Kitayama, 1991). Among the Ifaluk in Micronesia, the emotion word *fago* refers to a loving, wistful, empathetic form of compassion (Lutz, 1982); a prototypical example of *fago* is the caring, interdependent link shown by a mother tending to a sick child (Nuckolls, 1998).

Here, cultural neuroscience has the opportunity to capitalize on existing ethnographic work by employing a complementary experimental approach. In its simplest form, such an approach would work with local participants (in Japan, Micronesia, or elsewhere) to develop a set of stimuli that most reliably trigger the subjective state of *amae*, *fago*, or other apparently culturally specific emotion terms. Functional neuroimaging could help determine if such stimuli have a unique neural signature, and cross-group comparison could determine whether this neural signature was somehow either accentuated or showed unique attributes for individuals from cultural environments in which *amae* (or *fago*, etc.) was a recognized category of emotion. Ideally, such a research project would work with anthropologists and local participants to build a set of stimuli that properly represents the emotional referent at hand. Anthropologists have developed tools to ascertain both agreement (Weller, 2007) and diversity (Hruschka et al., 2008) in cultural models. As a preparatory step, such tools could be applied to assess the degree to which certain emotion terms are indeed broadly representative of subjective experiences in the local population.

Emotions, of course, are not just automatic responses to certain types of stimuli, but are subject to meta-awareness and appraisal (Ochsner and Gross, 2005), which can lead to processes of regulation (e.g., accentuation or suppression of associated facial expressions, behaviors, and subjective states). These appraisal and regulatory processes seem to rely especially on the prefrontal, orbitofrontal, and anterior cingulate cortices (Ochsner and Gross, 2005).

As well as having sites of neural control, appraisal and emotion regulation also have sites of social control. The drive to engage in such regulatory processes hinges on both direct social sanctions and the individual embodiment of social messages about how "bad" or "good" it is to experience or express certain emotions. For example, Harkness and Super (2006) show how cross-cultural variation in parenting strategies inculcates different patterns of emotional regulation in children (e.g., the emphasis on quietness and self-regulation in Dutch society). Similarly, Tsai et al. (2007) shows how East Asian cultural environments inculcate the sense that feeling calm is an ideal emotional state, while the cultural environment of child rearing in the United States valorizes states of high arousal.

Anthropologists are well positioned to identify the social circumstances that entrain this cultural variation in preferred emotional states and associated behaviors. For example, Miller et al. (1996) describe how a Taiwanese mother shames her son for displaying inappropriate emotions, by co-narrating a story with him about how embarrassing and inappropriate it was for him to cry in public. As Shweder (2003) points out, such differences in the social context of emotion can affect the deep phenomenological features and behavioral concomitants of emotion; shame can become an emotion that is subjectively perceived and popularly espoused to be a social virtue, as among the Oriya Brahman caste.

The cumulative body of evidence that certain affective states may be preferred differentially across societies flies in the face of presumptions that specific emotions are inherently and inexorably pleasurable or aversive. Instead, the subjective experience of affective states is at least partially encoded by the forces of culture. Emotional states that share surface (and perhaps psychobiological) similarities are thus perceived, appraised, and experienced differently across groups and individuals. Such differences in preferences and social sanctions around affective states contribute to cultural variation in the way that psychological distress is experienced and manifested (Kirmayer, 1992).

The cultural value placed on ideal and appropriate emotional states not only affects the experiences that individuals seek out (Tsai, 2007), but also affects more immediate regulation of facial displays of emotion (Matsumoto, 1990). Experimental work has shown that deliberate suppression of emotional expressions (particularly anger and disgust) takes a physiological toll, increasing sympathetic peripheral nervous system activity (Gross and Levenson, 1993). Furthermore, experimental research indicates that intentional positioning of facial expressions feeds back to the central nervous system, affecting subjective perceptions of emotional state (Adelmann and Zajonc, 1989).

The pressure to inhibit or display certain affective states and associated behaviors is structured by common social forces such as gender and social status (Keltner et al., 2003). Moreover, such pressures are rearranged over time as communities experience modernization, globalization, and other forms of cultural and social change. Anthropologists are particularly adept at documenting how culture works to encourage or discourage affective states and related behaviors. For example, Fry (1992) documented how differential child socialization and community differences in social reinforcement for aggressive displays were associated with strikingly different levels of violence in two neighboring Zapotec communities.

An experimental approach using functional neuroimaging could determine whether cultural differences in the appraisal, valuing, and intentional regulation of different emotional states and associated facial displays results in detectable group differences in patterns of neural activity. Anthropological input would be particularly useful in generating hypotheses regarding the differential expectations for (or stigma placed on) particular emotional states across race-ethnicity, social class, gender, nation-state, and cultural group.

As previously noted, anthropological research is particularly useful for identifying the cultural scripts, social sanctions, and socialization practices that inculcate an embodied sense of certain emotional states as ‘‘proper’’ or ‘‘ideal.’’ Detailed ethnographic observations also suggest putative causal mediators in the relationship between culture and affect, shown by Harkness and Super’s (2006) work on parental ethnotheories for child affect regulation. Cultural neuroscience could make use of these putative causal mediators, moving beyond intergroup comparisons to examine the relationship between *socialization experiences* and patterns of neural response to stimuli. Due to intensive data collection and local knowledge, anthropological research often identifies subnational or subregional variation in emotion and related outcomes. These local comparisons could be of use to cultural neuroscience, especially as two neighboring communities are likely to share historical, ecological, genetic, and other factors that would otherwise confound comparisons across groups vastly separated in geographic space.

Dominance, power, and social hierarchy

Every society has some method for sorting individuals by social status (whether explicit or implicit), and this has deep evolutionary roots (Mazur, 2005). However, the content, form, and process of social hierarchies in different societies vary immensely. In one society, a high status individual is marked by a large belly and sizable collection of pigs, while another society marks high status with extremely thin mobile phones and ‘‘washboard’’ abdominal muscles. The variety of behaviors used to invoke or signal differential power are just as variable; a warlord might assert power through occasional raids on neighboring villages, while college acquaintances might vie for power through aggressive joking and teasing. Furthermore, many human societies work to deliberately conceal the workings of power; for example, the cultural script of meritocracy and the American Dream in the United States means that the exercise of power often takes covert forms. Other societies obfuscate the workings of power by invoking divine ordination for powerful human figureheads.

While the workings of social status and power are immensely variable and complex, their impact is clearly felt and exhibited in the biology and behavior of individuals. Perhaps the strongest evidence of how differential status and hierarchy is represented in individual biologies comes from the socioeconomic gradient in human health. A study by Marmot and Smith (1997) first illustrated this among civil service employees in the United Kingdom, among whom a strong status gradient (based on civil service rankings) in cardiovascular disease was found to exist above and beyond the effects of direct material conditions (such as salary), or health behaviors linked with socioeconomic status. A wide variety of studies have built on this finding, and there is some evidence that the extent of power differentials between individuals carries an additional element of health risk (Wilkinson, 1997). Although there is certainly debate about the precise causal mechanisms at work (Kroenke, 2008), social status seems to exerts its impact on health gradients at least partially via representations of relative social status in the brain. Recent neuroimaging evidence supports this; specifically, self-ratings of subjective social status were found to be associated with morphological differences in the anterior cingulate cortex (Gianaros et al., 2007).

Endocrine evidence indicates that the dynamics of power play out symbolically and can occur across immense distances in time and space. For example, simply watching one's favorite sports team win or lose an event on television leads to significant changes in cortisol and testosterone (Bernhardt et al., 1998), and similar patterns of response can be observed for winning or losing a chess match (Mazur et al., 1992). This provides direct biological evidence that the dynamics of power work themselves out symbolically, and need not involve direct participation in status competition itself. Similarly, social systems arranged along gradients of status marked by physical attributes — such as skin color — find their way into the workings of the brain, often without being consciously recognized. A good example of this is the frequent co-occurrence of high egalitarian values with high unconscious racial bias (Devine et al., 2002). Ingroup–outgroup dynamics create racial disparities in health (Adler and Rehkopf, 2008), and this seems to operate partially via the impact of social exclusion on biological functioning (Cacioppo et al., 2003). Notably, experimental investigations of social exclusion show that it is represented in the brain much the same way as physical pain (Eisenberger et al., 2003).

Anthropological studies of power have much to add in our investigations of the way that status and hierarchy are represented in the brain across different cultural settings. For example, cross-national and anthropological work reveals that the relevant "currencies" that figure into individuals' ratings of subjective social status differ markedly cross-culturally. For example, youths in the rural American South mark social status with currencies such things as having a recreational vehicle or having moved out of the parental home (Brown et al., 2008). Evidence of cross-cultural differences in the currencies of social status speaks to an important role for anthropological work in cultural neuroscience; developing culturally relevant and ecological valid stimuli that invoke relevant axes of interest (in this case, power, status, and hierarchy). For example, it appears that the ladder metaphor used in the MacArthur subjective social status measure (Adler et al., 2000) might translate better as a "glass" in Nepal (Kohrt, 2009). Designing the appropriate measure and associated stimuli to invoke notions of power (whether they be livestock, slim cell phones, or other symbols) is crucial for designing experimental protocols in functional MRI experiments with non-Western groups.

Anthropology has often focused on multiple forms of social power. Every society is replete with multiple status hierarchies; a gang leader may bow to the authority of a powerful apartment block representative, and the junior faculty member who was shouted down at a faculty meeting may later dominate the department chair in a game of intramural basketball.

The forces of modernization and globalization make it more likely that individuals "measure up" differently across competing dimensions of status and power. Anthropological work has operationalized this phenomenon as status inconsistency, and has shown that such disjunction in ranking across multiple systems is related to biological and psychological distress (Dressler, 1988; McDade, 2002). Due to its demonstrated biological and psychological effects, the unique impact of disjunction in ranking across multiple forms of hierarchy would likely be detectable at the level of the central nervous system. Collaborative work between cultural neuroscience and anthropology would help develop research locales and experimental paradigms designed to assess the particularly stressful nature of status inconsistency.

Anthropologists have also noted the existence of group differences in the extent to which social hierarchy is enforced — or in some cases actively discouraged and sanctioned *against.* For example, certain hunter–gatherer societies maintain relative equality via active and stringent social controls against the unequal distribution of goods or displays of arrogance or authority (Woodburn, 1982). The maintenance of such social systems requires a strong internalized sense (transmitted across generations) of strict egalitarianism as the "right" or "just" state of being. Whether one believes (or not) that a drive toward selfishness, inequality, and hierarchy is an inevitable facet of humanity or not, it is likely that such a strong system of social controls and the existence of cultural models for equality affect the way that social relationships are represented in the brain. For example, it is possible that the representation of subjective social status in the anterior cingulate cortex (Gianaros et al., 2007) would be less apparent in such a population. Furthermore, if subjected to power differentials in a laboratory environment, such populations might also display more pronounced negative affect. These are, of course, open empirical questions, and present opportunities for the emerging field of cultural neuroscience.

Embodiment of social knowledge

Anthropologists have become increasingly interested in the concept of embodiment, or the idea that social and cultural meanings ‘‘get under the skin’’ in order to affect the functioning of human bodies. For example, there is the aforementioned evidence that meanings associated with relative social status affect health, evidence that symbolic qualities of therapeutic interactions and technologies influence healing (Moerman and Jonas, 2002), and evidence of the way that religious belief and practice affect health (Berntson et al., 2008). Anthropologists are also interested in the ways that social learning becomes embodied, or internalized in noncognized ways, such that everything from sensual experience (Kontos, 2006; Strathern, 1996) to the experience and expression of physical and emotional suffering (Kirmayer, 1992; Kleinman, 1980) is influenced by prior socialization and implicit cultural models.

Bourdieu has argued for the existence of a set of embodied, socially learned dispositions that function ‘‘on the practical level as categories of perception and assessment or as classificatory principles, as well as being the organizing principles of action’’ (Bourdieu, 1990). According to Bourdieu, this ‘‘habitus’’ is learned implicitly, through interaction with social structures, and it encompasses a host of noncognized ways of being in the world, including postures, tastes, and the production of socially prescribed action (Bourdieu, 1990).

How might such investigations intersect with cultural neuroscience? One pertinent area of research, with major implications for thinking about embodiment, has to do with mirror neurons. Mirror neurons seem to facilitate social cognition by helping individuals to understand others’ actions. It has also been argued that they may have evolved as a mechanism for imitation, a key form of learning for humans in particular (Iacoboni and Dapretto, 2006; Rizzolatti and Craighero, 2004). Some argue that there may be ‘‘a whole range of ‘mirror matching mechanisms’’’ in the brain, and that such mirroring mechanism may be intimately related to the nature and importance of our intersubjective experiences (Gallese, 2003). Given their utility for both social cognition and learning, it makes sense that mirror-matching mechanisms would facilitate social learning in particular. For example, there is evidence that mirror neurons are involved in the automatic imitation of others during social interactions (Iacoboni and Dapretto, 2006), which suggests that they may represent a mechanism for an implicit, embodied dimension of social learning and socialization.

In addition, a number of researchers have recently argued for a more general embodied model of cognition, in which knowledge is represented in part by the ‘‘original modality specific states’’ elicited by an experience, rather than in an abstract, symbolic form. According to such theories knowledge, including social knowledge, has an important sensorimotor component (Barsalou et al., 2005; Lakoff and Johnson, 1999). These more implicit, embodied forms of memory related to such a mirroring or simulation system (Barsalou et al., 2005) likely form the basis of the automatic social actions and embodied social attitudes described by Bourdieu (1990). For example, bodily postures held during the presentation of novel stimuli affect the attitudes toward those stimuli when subsequently displayed (Cacioppo et al., 1993; Niedenthal et al., 2005). Embodiment of certain kinds of postures and gestures, or learning a particular habitus, makes automatic these physical enactments of social knowledge, and can powerfully and implicitly reinforce certain social structures. Automatically lowering one's head in the presence of a superior reinforces the social "fact" of a status differential, and reinforces the subordinate rank of the head-lowering individual, for instance.

What the studies linking physical positions and attitudes do not address, however, is how one learns to associate such postures with emotional valence or other attributes in the first place. This kind of learning presumably employs the same embodied mechanisms. How does one come to associate pushing up on a table as an approach behavior, or nodding one's head as a gesture of affirmation? There is evidence that the cognitive referents associated with gestures are far from universal. For example, in both linguistic and gestural terms, the Aymara indicate the temporal future as *behind* the body, and the past in front of it (Nunez and Sweetster, 2006). Thus, while some gestural referents seem to be innate products of occupying a human body (Lakoff and Johnson, 1999), the cultural plasticity in such associations can be quite wide-ranging.

An experimental approach in cultural neuroscience has the potential to further illuminate the neural substrates and cognitive and emotional implications of such forms of social embodiment. For instance, cultural neuroscience could expand current research on the embodiment of category knowledge to include research on social and cultural knowledge. Several recent studies have shown that motor systems are activated by images of objects or words associated with particular action sequences. For example, when passively viewing a hammer, motor areas associated with grasping objects is activated, and passively viewing images of food items stimulates activation of brain areas known to represent how foods taste, as well as reward centers (Chao and Martin, 2000; Simmons et al., 2005). Similarly, words associated with the movement of certain body parts precipitates differential activation of motor areas — that is, "kick" activates areas associated with leg movements (Hauk et al., 2004).

Such research could be extended to include neuroimaging studies designed to investigate the activation of modality specific areas in response to social categories and cues. Questions of interest might include: when presented with particular social scenarios, are habitual or embodied social responses simulated in the brain? What happens when people are instructed to take on postures or engage in social gestures that violate their social status? How difficult (and/or stressful) is it for people to unlearn automatic or embodied social behaviors? Anthropologists are uniquely positioned to contribute fine-grained information about the connections among social status, social expectations, and embodied social behaviors, or habitus, for individuals from diverse cultural backgrounds, to be used in the design of ecologically valid experimental, and cross-cultural comparative study designs.

Ritual

An area in which the collaboration of anthropology with cultural neuroscience has particularly productive potential is the connection between embodiment and ritual. Anthropologists have long argued that ritual is a key mechanism of socialization; a means through which the important beliefs, concepts, and symbols of a society are invested with motivational force at the individual and group levels (Durkheim, 1995 (1915); Rebecca Seligman, 2005). One proposed mechanism through which ritual might accomplish such social conditioning is through its capacity to influence learning and memory formation. A number of anthropological theorists have argued that the sensory stimulation involved in rituals produces strong emotions that lend themselves to associative learning of the symbolic content of these ritual performances (Turner, 1983; Whitehouse, 2000). For instance, initiation rituals often induce strong emotions through employment of social isolation, novel locations, physical discomfort or pain (i.e., circumcision, scarification, sleeping on the floor, etc.), loud noises, rhythmic movement, drumming, exposure to brightly colored stimuli or painting of the body, etc. (Barsalou et al., 2005; Seligman, under review; Van Gennep, 2004 (1960)). Evidence from neuroscience supports the idea that certain kinds of sensory stimuli are especially likely to reinforce learning and produce mnemonic effects (LeDoux, 1998; Rolls, 1999).

Enhanced memory for content learned during rituals may also relate to the sensorimotor engagement involved in ritual, which lends itself to implicit, embodied forms of learning of the sort described above; learning and performance of coordinated group action, dance, initiatory trials, etc., are likely to engage mirroring and simulation systems within the brain. In fact, many elements of ritual practice appear to be designed to capitalize on the kinds of embodied effects on attitude that we discussed above (Barsalou et al., 2005). For example, prostrating oneself in prayer or in the presence of a spiritual leader may contribute to the experience of submissiveness to a spiritually powerful other. Similarly, frenetic movement in the context of ecstatic rituals may contribute to excitement, emotional arousal, and even openness to the experience of bodily possession by a spirit or deity (Seligman, under review).

The bodily practices frequently engaged in as part of ritual may also mean that ritual learning is encoded in multiple memory systems simultaneously (i.e., implicit, episodic, procedural). The emotional arousal associated with ritual participation means, for example, that what is learned during ritual is likely to be encoded and consolidated in special ways related to emotional memory. Evidence from neuroscience confirms that emotional arousal enhances memory, partly through short-term effects on encoding that may be mediated by attention, and through facilitation of longer-term memory consolidation by the amygdala (Ink, 2006; McGaugh, 2004). Emotional memory of this sort represents a form of embodiment, and is implicated in the vividness of emotional memories, and the experience of ‘‘reliving’’ powerful emotions in response to relevant cues (Heuer and Reisberg, 1990; LaBar and Cabeza, 2006). A number of studies have found that amygdala activation while viewing emotionally arousing films, slides, or scenes is highly positively correlated with subjects’ recall of the material several weeks later (Canli et al., 2000; Hamann et al., 1999). Moreover, it appears that greater emotional intensity of the material predicts stronger correlations between amygdala activity and encoding and activation (Anderson et al., 2003; McGaugh, 2004). These findings hold true whether the valence of the emotional material is positive or negative. Studies also indicate that the amygdala is activated during retrieval of both positively and negatively valenced emotionally arousing material (Dolan, 2000; McGaugh, 2004).

Collaborative efforts between cultural neuroscience and anthropology can lead to the design of studies that investigate the connections between ritual practices and emotional learning/memory, by designing creative protocols that allow amygdala activation to be measured during the encoding and retrieval of ritually salient symbolic material. A simple experiment would involve neuroimaging of amygdala activation during recall of a salient ritual in which subjects had participated several weeks earlier. Anthropologists with in-depth knowledge of ritual practices and access to spiritual adepts and leaders might also design more complex, interactive video protocols that simulate ritual contexts. These protocols could introduce new, salient ritual knowledge to religious participants in a laboratory setting in which brain activity could be imaged during encoding and again later, to examine the role of the amygdala in memory consolidation of this material.

Memory encoding and consolidation are also modulated by neurohormonal activity. Evidence from neuropsychological and neuroimaging studies suggest that the amygdala mediates beta-adrenergic enhancement of long-term consolidation of emotional memory and is functionally connected to arousal-related memory effects in the hippocampus as well (LaBar and Cabeza, 2006). Thus, measurement of adrenocortical activity tells us something about memory consolidation at the central level. Since hormone activity is fairly easy to measure in field settings (McDade et al., 2007; Worthman and Stallings, 1997) it could be used in studies designed to get a sense of how in situ ritual participation relates to neurohormonal activity associated with memory consolidation, vivid memories, etc.

The emotionally arousing properties of rituals can also be measured in situ using ambulatory psychophysiological measurement techniques to investigate the effects of ritual participation on things like heart rate, blood pressure, skin conductance, and the differential contributions or "balance" of the sympathetic and parasympathetic nervous systems in relation to cardiovascular activity in the context of ritual (Berntson et al., 2008). Use of psychophysiological measurement can answer questions about how the sensory stimulation techniques involved in ritual are reflected in autonomic activity — that is, how they are embodied by participants during participation in ritual. A study employing this research strategy in the context of religious practice and spirit possession mediumship in Northeastern Brazil, was conducted by one of the authors.

Conclusion

We have identified several areas of inquiry in which anthropology and cultural neuroscience could productively intersect. We suggested how anthropology might inform research in cultural neuroscience on emotion, via structured ethnographic work that maps the prevalence and meaning of emotional states. Furthermore, we argued that anthropological work can help identify neighboring communities that differ in affect and related behaviors (e.g., anger and aggression), and also suggest potential aspects of socialization that are responsible for these differences.

We then moved to the study of power, dominance, and hierarchy. The complexity and cross-cultural variability in social hierarchies (and the workings of power therein) makes anthropological work necessary to properly label the relevant *currencies* of status and power within communities (Brown et al., 2008). Such work is crucial the proper design of stimuli for use in experimental protocols. Furthermore, anthropological work can help identify when individuals differ in status across multiple, competing domains of status and power (McDade, 2002) — a phenomenon that seems to have a unique biological and psychological effect. Finally, ethnography has helped identify societies in which egalitarianism is the norm, as well as the ways in which this egalitarianism is socialized and enforced. Such groups would prove especially interesting for work in cultural neuroscience on how subjective social status is represented in the brain.

Partially rooted in the study of social class, anthropology has developed an extensive literature on the embodiment of social knowledge via aesthetic taste, posture, and other dimensions of human experience and behavior (Bourdieu, 1990; Strathern, 1996). Anthropology and cultural neuroscience could productively intersect on such issues via the design of experiments to examine the neural substrates of perceptions and social behaviors linked to the entrainment of social class, gender, and other social forces. Anthropological work describes how social systems help enculturate within and cross-group differences in ways of experiencing, perceiving, and behaving in the world. Future work in cultural neuroscience could focus more specifically on how exposure to these mediating influences affects the brain, rather than relying on broad group comparisons and associated putative cultural differences.

Finally, we discussed how the study of ritual could form a productive intersection for anthropology and cultural neuroscience. Specifically, ritual is an essential mechanism for the inculcation of cultural knowledge, and can have a profound impact on behavior and emotion. Furthermore, the experiential elements of ritual seem designed to invoke affective reactions and to link these with cultural expectations about appropriate feelings and behavior. The unintentional "design" of such affective and behavioral entrainment is mediated by emotion's memory-enhancing properties, which in turn have neural substrates. Collaborative work between anthropology and cultural neuroscience should focus on these biocultural design elements. Furthermore, collaborative work between anthropology and cultural neuroscience could involve field studies in which the endocrine and peripheral nervous system concomitants of ritual can be studied in situ.

We anticipate a rich and productive collaboration between anthropology and cultural neuroscience.

The rich knowledge generated by ethnographic work describes hidden but meaningful complexity in the lives of individuals. Anthropology's presence in diverse cultural settings also suggests interesting case studies for cultural neuroscience. And, anthropology's emphasis on the embodiment of social knowledge (especially via ritual) suggests new sites for the investigations into how the social world gets not only under the skin, but also into the brain. With an emerging set of tools to operationalize and quantify the workings of culture (Hruschka et al., 2008; Weller, 2007), such productive intersections are bound to grow more fruitful with time.

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CHAPTER 4

The brain in culture and culture in the brain: a review of core issues in neuroanthropology

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Abstract: Neuroanthropology is a new field of research that can make two distinctive contributions to our understanding of the brain-culture nexus. The first contribution has to do with the question of how socially shared meanings and practices are reflected in brain function and structure — the culture in the brain problem. Neuroanthropology's second contribution relates to the neural processes that generate socially shared meanings and practices — the brain in culture problem. Research in cultural neuroscience has focused on the first question while research in social neuroscience has a bearing on the second. A neuroanthropological perspective is vital to integrate these two most important dimensions of the human condition. In this paper we review research from cultural anthropology, primatology, and developmental psychology, in addition to social and cultural neuroscience, that deals with these two core neuroanthropological issues. Regarding the brain in culture problem, the review reveals that relational recoding is the basis of a host of cognitive functions that enable the formation of socially shared meanings and practices. The review also shows that relational recoding corresponds to the processing style characteristic of the prefrontal cortex (PFC). With respect to the culture in the brain problem, the most salient finding is the extent and breadth of the influence of culture on the brain: literally all brain areas, cortical and subcortical, respond to regularities in the cultural stream of experience. Furthermore, culture not only shapes preexisting patterns of neural activity but it may also determine whether a pattern is at all present. In addition to influencing brain function culture also changes the structure of the brain. The review finally indicates that cultural regularities can modulate cognitive function both implicitly and explicitly. Overall, the PFC can be regarded as the structure that establishes relationships between things and events that are represented in the different areas distributed across the brain. These areas become in this manner more readily available for modulation or constitution by (cultural) experience. However, the PFC is the structure that stands first to be modified or constituted by cultural experience as it is the structure that lays culture's foundations.

Keywords: neuroanthropology; brain; culture; relational recoding; prefrontal cortex

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Introduction

Neuroanthropology is a field of study closely related to social and cultural neurosciences that theoretically and methodologically integrates anthropology and neuroscience to study the poorly understood relationship between culture and the brain (TenHouten, 1976, 1992; d'Aquili et al., 1979; Laughlin et al., 1990; Turner, 1985, 2001; Domínguez et al., 2009). Conceived as a humanistic science, neuroanthropology is founded on the recognition of a fundamental interdependence between the interpretive/context-dependent/particularistic forms of inquiry of the humanities and the nomothetic/context-independent/analytic forms of intelligibility used in science (Domínguez et al., 2009). We have previously indicated the need for research in this field to combine ethnographic fieldwork with the experimental techniques and methods of social and cultural neurosciences. As a rationale for this research paradigm, we have argued that the study of the culture–brain relationship requires, first and foremost, an understanding of cultural activity, which can primarily be acquired by means of the naturalistic and interpretive, yet empirical, methods of humanistic anthropology. We should note that anthropology has also a robust scientific tradition, present not only in studies of cultural activity and society but also in other anthropological domains such as evolutionary and biological anthropology as well as cognitive anthropology. This tradition can be used as a bridge between the neurosciences and the humanistic dimension of anthropology.

We regard neuroanthropology as being dependent on and complementary to social and cultural neurosciences, and have argued (Domínguez et al., 2009) that it has the potential to make a number of distinctive contributions that include: (1) insights into the ways cultural activity unfolds in naturalistic settings and the possibility to better characterize cultural processes that affect brain function and structure; (2) a heightened sensitivity to issues related to ethnocentric biases; (3) an increased ecological validity of research findings in combination with cross-cultural research; (4) in addition to cross-cultural diversity, attention to intracultural variability, as well as culture-related peculiarities of individual brains; (5) expanding ethnographic, archeological, and paleoanthropological records that can be used to identify phenomena for experimental research, derive hypotheses, and contextualize findings; (6) an opportunity to use neurometric data to aid in the interpretation of meaning and intention; (7) the possibility to use these same data to guide theorizing about social and cultural models; and (8) an increased understanding about the full extent of the epistemological processes leading to pragmatically valid knowledge.

One last distinctive contribution of neuroanthropology is its broader scope of inquiry, which includes not only culture in the brain, that is, the ways socially shared meanings and practices are reflected in brain function and structure, but also the brain in culture, the neural mechanisms enabling those meanings and practices — their phylogeny and ontogeny. Research in cultural neuroscience has focused on the first problem. While not explicitly its focus of attention, a good deal of research in social neuroscience has a bearing on the second problem. A neuroanthropological perspective is vital to integrate these two most important dimensions of the human condition, which we should expect to be complementary or, in other words, to have coevolved phylogenetically and to codevelop ontogenetically.

In this paper, we review research from a range of fields including cultural anthropology, primatology, and developmental psychology, in addition to social and cultural neurosciences, that deal with these two core problems in neuroanthropology. We devote two-thirds of this paper to the brain in culture problem, as it has remained largely unexamined. The remaining one-third of the paper consists of a review of studies providing an insight into the issue of culture in the brain. This latter part includes but goes beyond current cultural neuroscience research and its exclusive interest in cross-cultural investigations. The review also comprises studies looking into different domains of cultural activity such as expertise, political ideology, and religious practices.

The brain in culture: how the brain generates culture

Culture can be broadly defined as the repertoire of socially generated behaviors typical within a group of interrelated individuals (Laland and Hoppit, 2003). From this perspective, there is evidence that behavior patterns exhibited by a range of social species are cultural — including location–behavior associations in fish (Helfman and Schultz, 1984), dialect variants of bird song (Catchpole and Slater, 1995; Janik and Slater, 2003), synchronized change in song between many individuals in Humpback whales (Rendell and Whitehead, 2001), preening together in fowl (Hoppitt et al., 2007), seed feeding and gathering procedures in rats (Terkel, 1994; Galef, 2003), location of water and salt sources in elephants (Viljoen, 1989; Redmond, 1982, 1985), and social conventions in monkeys (Perry et al., 2003). However, culture is almost always exclusively discussed with reference to the one species that has made a virtue of cultural production, reproduction, and transformation, that is, the human species. Culture in humans is not only orders of magnitude more complex, multifarious, and generative than in any of the other species for which culture has been reported, but also qualitatively different from animal culture. The difference between human and animal culture lies in the fact that while, in animals, culture involves the rote and unreflective sharing of a limited range of stimulus–stimulus or stimulus–response associations, human culture is based on intersubjective and reflexive understanding facilitated and largely mediated by a capacity to manipulate symbols.

Widely acknowledged in anthropology is that the world of human cultural activity is not an objective world that can simply be observed from the outside. Its existence cannot be conceived independently from the meanings by which it is accounted for, and in fact, constructed by people. Physical movement is observable. However, individuals do not just move (or behave); they act. The distinction between movement and action is fundamental. The meaning ascribed to movement is what transforms it into action. But meaning is not observable. The same movement may correspond to different actions by virtue of its meaning. What “limits the scope of possible meanings are preconceived criteria which the actors have [and share] and which they apply to their actions” (Holly, 1984, p. 28) in particular settings. The ascription of meaning is therefore an inferential undertaking. It requires in the first place what has been referred to as individuals’ natural attitude of reciprocally attributing to each other subjective, intentional action; in other words, intersubjectivity – in itself a fundamental inferential accomplishment (Tedlock, 1991; Linger, 1994; Jackson, 1999). Symbols also play a fundamental role in figuring out intentional, meaningful action, since they constitute the signposts of intentions and meanings. They can also be regarded as the currency by which shared understandings are negotiated. People have only direct access to the symbol-tokens used by others in communicative acts, and they have to use what they know about these tokens and the context of their occurrence (their history of previous usage, the specific situations in which they occur, and their relationships to other practices and symbols relevant to them) to infer the tokens’ meanings. Only when the configuration formed by a given behavior or a symbol-token and its context is grasped can one be said to have understood its meaning. When encountering meaningful, intentional action, individuals generate what to them is the best estimate as to its meaning. To use an example made famous in anthropology by Geertz (1973), telling the difference between an eye twitch, a wink, and a mock wink (three behaviors with identical surface form) can only be done by considering the context in which they are encountered. Their import will be appreciated by those who are prepared to interpret them; they can be understood in a potentially infinite number of ways (or misunderstood) depending on different levels and ways of preparedness in those who come across them. From this perspective, culture can be said to correspond to the criteria that would lead different individuals to interpret, say, a mock wink, as such. More generally, human culture can be defined as the shared webs of interpretive criteria, of signification, in which human beings are caught but which they also spin (Geertz, 1973; Scholte, 1984).

In what follows, we will discuss first, but briefly, the neural mechanisms underpinning nonhuman animal forms of culture. We then review research that sheds light on the neural basis of intersubjective understanding and symbolic capacity, which we identified above as the defining enculturative mechanisms in humans. Moreover, we will propose that these two components of what could be termed as the human cultural adaptation are manifestations of a more basic process that we refer to as relational thinking.

Associative and mimetic mechanisms

Most of the examples of cultural behavior in animals quoted above have been explained by three simple mechanisms of social learning, known as stimulus enhancement, goal emulation, and response facilitation (Byrne and Russon, 1998). These mechanisms can be described simply as changes in the salience of stimuli, goals, and responses after observing the actions of another member of the group at a place or in conjunction with some objects.

The above mechanisms lead to the formation of local behavioral traditions in the absence of any understanding of the instrumental relationships that link a sequence of behaviors to each other and to their outcome, that is, without imitation. These traditions or cultures emerge, instead, as a simpler and more common individual learning and exploratory mechanism of trial and error that becomes biased by stimulus enhancement, goal emulation, response facilitation, or a combination of these. This was demonstrated experimentally in a study where a food-washing tradition emerged among two groups of primates in less than 2 hours (Visalberghi and Fragaszy, 1994). The experimenters, who gave fruit coated with sand to capuchin monkeys and macaques, observed that individual animals exhibited exploratory and playful behaviors with the food. This behavior eventually led them to bring the dirty food in contact with water where it would coincidentally be washed clean. Gradually, each individual recognized the link between washing and more palatable food. The authors note that the acquisition of this behavior was not accelerated from observing others. Rather, an enhancement mechanism was at work with observation of conspecifics affecting the behavior of individuals ‘‘by attracting their attention to the water, and some times to the fruit’’ (p. 259).

Stimulus enhancement, goal emulation, and response facilitation have been cognitively explained in terms of associative learning (i.e., classic and instrumental conditioning) and priming. They all involve increasing the activation of internal representations of environmental features, goals, and responses that cooccur with the sight of a group member gaining a reward (Byrne and Russon, 1998). Providing a full account of the neural mechanisms underlying associative forms of animal culture is beyond the scope of this paper. Here, we will briefly refer to the case currently best understood, that is, response facilitation in the macaque. Byrne (2003) has proposed that the neural mechanism of response facilitation corresponds (at least in part) to the activity of the mirror neuron system as identified in the macaque brain. Mirror neurons, found in a frontoparietal network that comprises areas F5 and PF of the macaque brain, are characterized by activity both when an individual performs a simple goal-directed action (like grasping an object) and when the individual observes another performing the same action (Rizzolati and Craighero, 2004). According to Rizzolati and Craighero (2004), the mirror neuron system mediates the understanding of action simply by automatically activating the neural representation of an action already present in the repertoire of an individual when he or she observes a similar action being done. In other words, the mirror neuron system is involved in the recognition of others’ movements by matching them to one’s own inventory (see also Paukner et al., 2004; Iacoboni, 2005). According to Byrne (2005), response facilitation is the result of combining the mirror neuron system’s capacity to recognize a familiar action being performed by someone else with a tendency to do the same thing oneself.

Mirror neurons may also be implicated in what we would call mimetic forms of animal culture — including regional variants of bird song, sound imitation by mynas, lyrebirds and parrots, and social mirroring. Mimetic forms of culture correspond to the rote, additive, detailed, and linear reproduction of a sequence of behaviors, or what Byrne and Russon (1998) have called action-level imitation. This form of imitation, perhaps better referred to as mimicry, does not involve the reproduction of novel behaviors, the recognition of hierarchical relationships among the components of action, or instrumental understanding of the sequence of movements copied. Byrne (2003) has suggested that the mirror neuron system may mediate action-level imitation by allowing an observer to segment the continuous flow of movements performed by another individual into its constituent components, provided these components are present in the behavioral repertoire of the observer. In this scenario, mirror neurons are simply responding to familiar movements, or movement segments, which would result in those segments emerging from the continuum of action. According to Byrne, if observing a sequence of familiar actions also makes it possible to string them together, then action-level imitation may take place.

We should finally note that the superior temporal sulcus (STS) is likely to play an important role in associative and mimetic forms of culture. Just as mirror neurons in F5 and PF, these neurons become active when observing goal-directed actions done by others. Unlike mirror neurons, however, STS neurons do not have motor properties (Perrett et al., 1989, 1990; Jellema et al., 2000, 2002). They can be thought of as coding the visual representation of observed action. Iacoboni (2005) has proposed that, given their functional properties and connectivity patterns (F5 and PF, and STS and PF are anatomically connected), these three areas could be considered to constitute an action recognition system. This system can be regarded as the core neural mechanism of associative and mimetic forms of culture – at least in primates; mirror neurons have been identified in the swamp sparrow (Prather et al., 2008), but an action recognition system remains to be characterized in birds.

Relational thinking and recoding

Associative and mimetic mechanisms are sensitive only to regularities discoverable by simply attending to directly observable relative frequencies of events. In other words, these mechanisms can unveil one-to-one correlations between two types of stimuli (classical conditioning) or between a behavioral response and its outcome (instrumental conditioning). However, other behavioral statistical regularities are a function of the relational properties of the variables that produce them and can only be identified in a derived way, that is, by some systematic recoding of the input features, whereby the relational properties among them are defined as new, higher-order features. Finding a recoding solution is the key operation, as it is the mechanism by which a relational property is transformed into a higher-level element that renders previously complex and elusive properties into simple patterns (Clark and Thornton, 1997).

Consider the two sequences ABCBAC and DEFEDF. They share no common surface structure but they have in common an abstract isomorphic relational structure that can be recoded as /u, u, u, $n-2$, $n-4$, $n-3$/ where u indicates random or nonrepeated (Dominey, 1997). A clearer illustration of recoding is the following example by Clark and Thornton (1997). The set shown in Table 1 comprises two input variables (x_1 and x_2) and one output variable (y_1). A direct inspection of the conditional probabilities from this data set, that is, $P(y|x)$, shows that they are close to their chance values — for example, $P(y_1 = 1| \ x_2 = 2) = 0.67$. However, the input variables in each sample pair can be recoded as a single variable, x_3, the value of which is a function of the magnitude difference between x_1 and x_2 (see Table 2). The recoding of x_1 and x_2 into x_3 allows us to predict the value of the output variable y_1 with certainty. Thus we can predict that $y_1 = 1$, if the difference between x_1 and x_2 is 1. We can also predict that $y_1 = 0$, if the difference between the input variables is 0 or 2. In this

Table 1. Original data set for input variables x_1 and x_2, and output variable y_1

x_1	3	2	3	3	2	1
x_2	2	2	2	1	1	1
y_1	1	0	1	0	1	0

Note: Data sets for variables x_1, x_2, x_3 and y_1.

Table 2. Derived data set for recoded input variable x_3 and unchanged output variable y_1 (after Clark and Thornton, 1997, p. 59).

x_3	1	0	1	2	1	0
y_1	1	0	1	0	1	0

Note: Data sets for variables x_1, x_2, x_3 and y_1.

example, regularities between two input variables and one output variable can only be found by a recoding function that captures the relationship between the variables — in this case, the recoding function is the difference between x_1 and x_2.

In this section, we argue that cognitive and neural mechanisms that enable human culture, defined as intersubjective understanding and symbolic capacity, are in essence relational learning mechanisms able to generate and detect (by means of recoding) highly distributed, hierarchical, and nonlocal patterns of behavior. We review a number of cognitive capacities that appear to emerge sequentially during evolution and development and that lead to intersubjective understanding. Symbolic capacity is conceived in this paper as contributing to, but different from, intersubjective understanding, as the latter can occur in the absence of the former. We also contend that the prefrontal cortex (PFC) is the brain structure in charge not only of recoding information but also of recognizing and generating recoding functions, that is, of appreciating relationships between things.

Program-level imitation

Program-level imitation corresponds to the reproduction of the structural organization of a complex procedure (comprising a sequence of stages hierarchically related) without replicating the exact details of activity (Byrne and Russon, 1998). As naïve individuals are repeatedly exposed to the procedure, they first segment the string of activity into its component blocks. They do this by matching observed goal-directed behavior to their own existing repertoire of behaviors in the same manner as during response facilitation and action-level imitation. The action recognition system should be, therefore, expected to play an important role in this regard. Identifying the blocks of activity is, however, not enough for reproducing the procedure. The crucial step in program-level imitation is, we would suggest, finding a recoding function that allows individuals to pick up (and subsequently reproduce), from very noisy streams of activity, the structural and hierarchical relationships between the blocks of activity. The kind of information that is necessary and sufficient to do this is the goal structure of the procedure, that is, the relationships between subgoals and the overall goal.

We offer as an example the case of nettle preparation among mountain gorillas (Byrne and Russon, 1998). A gorilla is presented with various nettle plants, with the goal being to pass the nettles through its lips and eat them. In between, the gorilla must strip leaves from the stems, accumulate a desired amount of leaves, remove the debris, and fold the leaf blades. Sections of the procedure are iterated regularly to a criterion, and stages that prove unnecessary are omitted. This demonstrates an understanding of the hierarchical relationships between the different goals. Additionally, each individual gorilla has an idiosyncratic manner of achieving each small change, which shows that what they learn is the overall goal structure rather than the details of action. Byrne has proposed that sequencing, iteration, omission, and hierarchical structure, the cardinal aspects of program-level imitation, are extracted from statistical regularities in repeated action. In line with our argument for relational thinking, we would add that these regularities, being a function of the relational properties of the variables that produce them, can only be discovered by a recoding that defines their relational properties as higher-order features.

Goal sharing

Program-level imitation requires only understanding of conspecifics as animate and goal-directed entities. However, it has great limitations in terms of generative capacity, flexibility, and efficiency. Evidence suggests that, starting at nine months of age, human infants manifest cognitive capacities that go beyond program-level imitation as they become sensitive to the fact that other people monitor the success or failure of their own attempts at achieving a goal (Tomasello et al., 2005). An illustration of this capacity is the study by Behne et al. (2005; see also Csibra et al., 1999, 2002; Gergely et al., 1995; Carpenter et al., 1998) in which adults were made to give toys to infants but occasionally failed to do so. They failed in one of the two ways: sometimes the adults showed unwillingness to give the toy, but in other instances they acted as if they were trying but unable to give out the toy. Behne and collaborators found that babies aged nine months, but not six months old, exhibited signs of impatience when adults were unwilling. This demonstrated that nine-month-old infants have the ability to infer "from various aspects of behavior and context" an adult's unobserved, unaccomplished goal. The inference requires a recoding of available information to form a plausible explanation as to the behavior of the adult.

The ability of interactors to perceptually and mutually monitor their goal-directed behaviors allows them to share their goals. These goals serve to coordinate joint activity by providing a window into what each interactor perceives and their dispositions to behave. This form of social engagement has been called triadic by Tomasello et al. (2005) as it comprises the sharing of goals with respect to some external entity.

Attribution and sharing of intentions

In addition to understanding and sharing goals, infants are eventually (at about 12 months of age) able to understand that others have alternative plans of action and that they choose among them in the pursuit of a goal. Infants can at this stage understand intentions, which can be defined as including both a means (action plans) as well as a goal (Tomasello et al., 2005). Demonstration of this comes from a study by Gergely et al. (2002) in which preverbal infants saw an adult trying to turn on a light with her head. Half of the infants observed an adult performing this action with her hands occupied. For the other half the adult's hands were free. When imitating this action (without their hands being occupied), infants who saw the hands-free demonstration were more likely to turn on the light with their heads. Infants apparently reasoned that if the adults had their hands free and still turned on the light with their heads they must have intended to specifically do that. By contrast, if the adults' hands were busy, then the use of the head was deemed no longer as necessary and infants would simply turn on the light with their hands.

This study shows that infants have the ability to understand that actors perceive and evaluate the efficacy of their goal-directed actions in a rational manner. An understanding of an individual's own plan of action and that of an interactor's (from their perspective) in the pursuit of a common goal are the prerequisites for joint cooperative action (Bratman, 1992; Tomasello et al., 2005). This, in turn, requires that both participants' plans of action be embedded in a joint plan, itself subsumed to a structure of complementary individual or shared subgoals, and to the overall purpose of joint activity. All these operations correspond to the iterative recoding of activity at higher and higher levels of abstraction: from strings of behavior, to sub- and superordinate goals, to an interactor's plans and goals, to shared plans and goals.

Symbolic reference

Program-level imitation, goal sharing, and the attribution and sharing of intentions can be all regarded as belonging to the same group of cognitive mechanisms forming the basis of intersubjective understanding. Let us now look at the other capacity that is regarded as essential for human culture and that can be conceived more or less independently from intersubjective understanding. Symbolic reference has been traditionally characterized as an arbitrary and conventional token–object correspondence. According to Deacon (1997), beyond this arbitrary correspondence, the fundamental property of symbols is that they derive their referential capacity from the system of symbols of which they form a part. Thus, symbols have dual reference: they refer both to objects in the world and to other symbols. Crucially, symbols are able to refer to objects because they refer to other symbols; objects of reference can be identified through the semiclosed system of transformations or combinatorial possibilities between symbols. More specifically, the symbolic relationship between a sign-token and an object is a function of the relationship the former has with other sign-tokens, not just a function of the simple correlation between sign-tokens and objects (as with classical and instrumental conditioning). In symbolic reference token–object associations are recoded as relationships between symbols.

To exemplify the way symbolic reference operates, let us consider the following examples. A chimpanzee study by Thompson et al. (1997) illustrates symbolic reference with the simplest symbolic system of all: a two-symbol system. In this study, chimpanzees learned to represent the relational features (sameness and difference) of some inputs with an arbitrary external token (e.g., a heart for two identical objects, AA, and a dash for two nonidentical objects, CD). The chimpanzees had to understand the pattern of exclusion between the heart and the dash to be able to relate them back to their objects of reference. Thus, the token–object associations were recoded as token–token relationships. Supporting evidence that chimpanzees employed the tokens symbolically (rather than by conditionally associating tokens to objects) comes from a second task in which they were able to discover a higher-order similarity–difference relationship: a relationship between relationships (AA:BB or CD:EF). Not only the chimpanzees were successful in their performance, but they also managed to perform the task in the first try and without the aid of the physical tokens used in the original task. Presumably, encountering an identical (AA) or nonidentical (CD) sample pair activated the mental representation of the concrete token (heart and dash, respectively). When presented with the BB and EF alternatives, chimpanzees activated the corresponding mental representation and were in a position to covertly match this representation with the representation evoked by the sample.

The above-mentioned example is not intended to indicate a spontaneous cognitive ability in chimpanzees for handling symbols. Chimpanzees, in this example and from other studies (e.g., Savage-Rambaugh et al., 1978; Savage-Rambaugh and Lewin, 1994), are able to use simple symbolic systems due to special attributes of a very intensive training regime, which provides them with external support to shift attention away from one-to-one conditional associations between tokens and objects to the many-to-many relationships between the tokens (Deacon, 1997).

An example of symbolic reference from everyday human experience concerns how people figure out the meaning of kinship terms. The reference of kinship terms is to an extent a function of the relationships of complementary exclusion and contrast between the terms. Knowing the referent for the English kin term *aunt*, for example, requires the tacit recognition of the kin types to which the term can and cannot refer. That is, the term can be used to refer only to female siblings of father and mother and to the wives of their male siblings, with the exclusion of all other types of relatives. Grasping the pattern of exclusions between kinship terms, that is, recoding the term–person associations as term–term relationships will allow people to map the terms onto the right relatives (not only their own but in general).

This procedure can be taken further to a higher level of abstraction, to extract likely dimensions of meaning along which symbols vary. Consider the componential analysis of kinship terms as developed in anthropology. The English term *mother* differs from the term *father* in the semantic dimension of SEX; *mother* differs from *daughter* in the dimension of GENERATION (the first belonging to the first ascending generation and the second to the first descending generation); *mother* also differs from *niece* in the dimensions of GENERATION and LINEALITY (the former being a lineal relative and the latter a collateral relative). An examination of the ways kin terms relate to each other will reveal the componential meaning of all kinship terms in English (Table 3). Thus, *mother* can be defined by the semantic

Table 3. Componential structure of US consanguineal core terms organized according to relevant dimensions of meaning

Generation	Lineal		Collateral	
	Male	Female	Male	Female
+2	GrFa	GrMo	GrUn	GrAu
+1	Fa	Mo	Un	Au
0	Br	Si	Co	Co
−1	So	Da	Ne	Ni
−2	GrSo	GrDa	GrNe	GrNi

Note: Mo: mother; Fa: father; Da: daughter; Gr: grand, and so forth (modified from Romney and D'Andrade, 1964).

features of [female], [lineal relative], and [first ascending generation], while *uncle* can be defined as [male], [collateral], and [first ascending generation]. The terms themselves have in this instance been recoded as the relationships between the dimensions of SEX, LINEALITY, and GENERATION. This recoding provides even greater clarity regarding the relationships between the different kin terms and, by extension, the various classes of relatives.

The most basic enculturative mechanism

Two outstanding questions are: which mechanism out of intentional state attribution/sharing and symbolic reference is the more basic? And, is one of them derived from the other? These mechanisms have been difficult to disentangle as they both start to emerge in childhood at about the same time. One may ask, however, can such complex and hidden phenomena as intentional states be understood without the aid of symbolic reference? Evidence suggests that this is possible. Simple relational problems can be handled by symbol-independent recoding mechanisms, as in the case of program-level imitation among gorillas. Nonetheless, representations of the behavioral components of plans formed by an individual can be said to stand in for or represent specific instances of those components. From this perspective, they can be regarded as precursors of symbols. However, phenomena with increasing hierarchical depth and complexity (such as human intentions) can be more easily handled by (fully) symbolic means. Symbols can subsume large numbers of exemplars of objects, events, and even relationships that can then be recoded at higher levels. That was the case in the example of the chimpanzees that were able to understand relationships between relationships of sameness and difference because they had, at their disposal, symbols representing both concepts. In any case, both intentional state attribution/sharing and symbolic reference can be clearly seen to be more elaborate instances of recoding mechanisms, and while it may be that intentional states of others can be understood without the aid of symbols, it is also true that symbols can be used to infer intentional states of increased complexity with greater efficiency. Furnished by symbolic reference, by language, intentional state attribution/sharing evolves into what has been called theory of mind (ToM), understood as a belief–desire psychology in terms of which individuals come to interpret each other's actions (Tomasello et al., 2005; to be discussed below in the section Neural Instantiation of Recoding).

Language

Shared intentionality entails the extension of cognition into the collective. It gives rise to cognitive communities (Donald, 2001) in which cognitive activity, procedural or representational, can occur in a collaborative and distributed manner among its members (Hutchins, 1995). A fully formed cognitive community, a human society, cannot, however, come into existence without symbolic reference and, more specifically, without a fully developed language (associated with an expert-level language use). From the perspective of symbolic reference as described above, languages (hand signed, spoken, etc.) are massive collections of symbolic systems with particular relationships of substitution and contiguity between symbols. A product of cognitive communities, language is highly distributed in the everyday practices that instantiate it. However, the relationship between language and cognitive communities (and their individual members) is not unidirectional but reciprocal. Their structure and patterns of change are codependent but not identical. No single individual possesses all the generative (or for that matter derived) knowledge of their language. Linguistic knowledge and expertise shared by an entire community are only statistically concentrated (Deacon, 1997).

From the above, it follows that language is not the product of a universal grammar hardwired in a language acquisition device, as originally proposed by Chomsky (1965). Humans do not deductively apply a universal grammar onto their experience of language to predict its structure. However, the rules of a universal grammar cannot be inductively inferred either because of the structural complexity of natural languages, reflected in its hierarchical depth and the highly distributed and nonlocal character of the regularities present in it. Additionally, these rules are not directly observable in the surface form of sentences (Gold, 1967; Deacon, 1997).

Natural languages require a form of inference that, rather than inductively inferring rules of use directly from the highly variable input (every single phoneme, syllable, word, phrase, or sentence), recodes that input into higher-order features governed by regularities more easily identifiable. That form of inference corresponds to what we have referred to here as relational recoding, of which symbolic reference is perhaps the finest example. In the standard language of inference, relational recoding can be identified with abductive inference, defined first by Peirce (1931–1958) as a natural form of inference that works from effects to causes, from individual instances to rules. Unlike deduction and induction, which proceed in a context-free manner, the hallmark of abduction is that it operates in a context-dependent way, whereby hypothesized causes or rules are inferred by reflecting on the relational linkages of some input to other relevant input, which can be of the same or different kind, and are present in the immediate context in which the input is encountered or in the background knowledge of the individual. In other words, abduction works by grasping these linkages, by finding a recoding function that reveals them. Thus, for example, if we hear that a professional cyclist broke a collarbone we can infer that he or she crashed while riding a bike during a race. It is not a logically valid inference but it is plausible given what we know about professional cyclists. This is precisely the inferential process at work in the examples of symbolic reference above. Inferring that *aunt* means female sibling of father or mother and their male siblings' wives is a function of the contextual relationships of exclusion between this term and all the other kinship terms.

Neural instantiation of recoding

As argued above, the basic cognitive mechanism for social generation and sharing of experience is recoding. Deacon argues that the PFC evolved to handle symbolic reference. While this is likely to be the case, it can be argued that the PFC is more generally adapted for recoding (cf. Robin and Holyoak, 1994). As suggested by the presence of program-level imitation in great apes and the cognitive processes associated to intention attribution/sharing, recoding can be performed in the absence of symbolic reference. Also, not only does the PFC possess recoding functions to handle moment-to-moment interaction, but socially available recoding functions can also be acquired (the case of explicit instruction, for example) and new ones can be internally generated. Next, we provide evidence of a prefrontal adaptation for recoding use, acquisition, and generation that would have become the predominant cognitive style during hominid evolution leading to *Homo sapiens*. In this regard, we closely follow Deacon's (1997) account for symbolic reference, but we have updated and extended it. We look into the comparative neuroanatomy of PFC in apes and humans. We also review animal ablation studies and human lesion and functional imaging studies.

Comparative neuroanatomy

Size. The mode of encephalization of humans is different from that of primates, as demonstrated by the human adult brain and body size allometric trend. Human encephalization follows the fetal primate trajectory, but the overall timing is altered so that the early phase is longer, whereas the postnatal phase is shortened relative to other primate trajectories. The human brain is larger than predicted for a primate of human size. However, the human brain is not uniformly larger. It is a highly heterogeneous organ, and the size of different structures deviates from the primate trend to different extents. Preliminary estimations indicate that PFC is two times larger than predicted for an ape brain of human size, a major increment particularly when compared to the respective values for the human motor cortex (35%) or the secondary auditory cortex (117%), the structure with the next largest relative expansion (Deacon, 1997).

The PFC itself has not homogeneously changed in size. For example, relative to the rest of the brain, Brodmann area (BA) 10 in humans is twice as large as expected for an ape brain of human size (Semendeferi et al., 2001). On the other hand, while human BA 13 is largest in absolute terms, its volume relative to total brain volume is not correlated among the apes. In fact, BA 13 in humans (and bonobos) represents 0.03% of total brain volume, compared to 0.06% in gibbons and the highest of 0.09% in orangutans. Semendeferi et al. (1998) suggest that the reduced relative volume of human BA 13 is due to an increased differentiation and associated expansion of orbitofrontal cortical areas.

Connectivity. These major deviations in the size of the human forebrain can be expected to be accompanied by changes in connectivity patterns and microanatomical parameters. Deacon (1997) has suggested that as a result of the relative enlargement of the PFC one should expect to find a greater proportion of PFC synapses in target structures compared to those formed by competing structures. Preliminary evidence in support of this prediction comes from a recent structural imaging study (Schenker et al., 2005) comparing frontal lobe gyral white matter (immediately underlying the cortex) and core white matter (remaining white matter) between humans and apes. Gyral white matter was found to be larger than expected in humans relative to other ape species, suggesting increased interconnectivity both within the frontal lobe and between it and neighboring cortical regions. Recent evidence indicates that, relative to other apes, human BA10 may form a larger number of intrinsic and extrinsic connections, especially with other high-order association areas (Semendeferi et al., 2001).

In brief, available neuroanatomical evidence supports the proposition that the human PFC plays a predominant role in brain activity. The PFC is allometrically larger and more highly interconnected. In addition, various PFC areas are now known to contribute differentially to these properties.

Neuropsychology of the PFC

Studies investigating cognitive deficits associated with targeted ablation in the prefrontal lobe in monkeys have revealed that dorsolateral PFC damage is associated with delayed alternation and self-ordered sampling tasks (Jacobsen, 1936; Passingham, 1985); ventromedial PFC damage impairs performance in delayed nonmatch to sample tasks (Mishkin and Manning, 1978); periarcuate prefrontal damage is linked to conditional association tasks (Petrides, 1982, 1985); and go/no-go tasks are associated with periarcuate premotor damage (Petrides, 1986).

In humans, people with lateral PFC lesions generally experience a loss of “supervisory attentional control” (Shallice, 1988). They are also impaired in their ability to represent, formulate, and carry out plans and sequences of actions, including sequences of spoken and written language. Patients with lateral PFC lesions have difficulty in completing sorting, self-ordered pointing, and delayed-response tasks as well as tasks involving phonemic and word fluency and solving puzzles (Grafman, 2002; Fuster, 2001). People with damage to the orbital PFC have been reported to be impulsive and lacking inhibitory control. They are also unable to suppress distractions (Fuster, 2001), and have trouble in modification and selection of appropriate responses (Dubois et al., 1995; Rolls, 1990). Lesions in the medial PFC lead to a reduction in spontaneity and in the ability to initiate movement. Medial

PFC damage is also associated with apathy and disinterest. On the other hand, brain imaging studies have shown increased activity in the anterior cingulate in tasks that demand sustained effort and focused attention (Fuster, 2001).

PFC activity is thus highly heterogenous. However, a number of cognitive processes are thought to be sub-served by the PFC, including short-term memory, attention, self-governance, and the spatiotemporal integration of cognitive processes. Deacon (1997) that has proposed other critical PFC functions are a special form of self-governance and attentional shift. The first one refers to the ability to inhibit the tendency to get stuck in simple correlations (characteristic of conditional forms of learning), a major evolutionary obstacle that needed to be surmounted before humans were able to detect the relational properties of stimuli. Self-governance can be achieved by means of the second mechanism whereby attention can be shifted away from conditional associations and directed to alternative relational ones. In addition, short-term memory needs to be robust enough to keep these alternative associations in mind for as long as it is necessary to either recode them by means of previously achieved recoding functions or find a new recoding function. Although short-term memory limitations apply to the number of items that can be held in mind at any given moment (the magic number 7±2), this can be somewhat eased by chunking (Miller, 1956). Evidence directly supporting the relational character of PFC function comes from a study by Waltz et al. (1999) who found that patients with "prefrontal damage exhibited a selective and catastrophic deficit in the integration of relations" (p. 119).

Regarding the role of each major prefrontal subdivision, the lateral PFC appears to be in charge of recoding exterior, physical, and predominantly visual or speech related, in other words, perceptual characteristics of stimuli, owing to dorsal and ventral lateral PFC connections to the dorsal (where) and ventral (what) perceptual streams, respectively (Faw, 2003). Orbital PFC and medial PFC have major connections with limbic areas. Orbital PFC and ventromedial PFC together represent a prefrontal extension of the subcortical extended-amygdala stream. The dorsomedial PFC, in turn, is a continuation of the dorsal hippocampal-anterior-cingulate paralimbic stream. Accordingly, the orbital PFC and ventromedial PFC seem to recode emotional aspects of experience and dorsomedial PFC appears to deal with motivational recoding.

Finally, Koechlin and Summerfield (2007) have proposed a cascade, or hierarchy of cognitive control that can be mapped onto the lateral PFC in a posterior to anterior axis. In this model, cognitive control, which the authors define as the ability to coordinate thoughts or actions in relation to internal goals, operates along three nested levels of control processes comprising contextual, episodic, and branching processes. Note that all these levels of control simply involve wider and wider forms of contextualization: from the present perceptual context in which stimuli occur (subserved by posterior lateral PFC), to the temporal episode in which the stimuli take place (coordinated by anterior lateral PFC), to pending episodes defined by information conveyed by preceding events (associated with polar PFC).

Derived and other associated neural mechanisms of recoding

Self-monitoring and auto-evaluation

Self-monitoring and auto-evaluation at perceptual and cognitive levels are central to the means-ends analysis of activity, which is in turn essential for intentional action. They are also cardinal in the production and reproduction of culture as they are one of the mediators of first, triadic, and, later, collaborative engagements (Tomasello et al., 2005). Monitoring and evaluating one's own intentional behaviors serves as a template to evaluate other peoples' behaviors. This is done in a reciprocal manner: individuals back-project other peoples' actions and dispositions onto themselves to guide their own behavior. Regarding the neural basis of self-monitoring and auto-evaluation, orbitofrontal patients are impaired in their capacity to determine whether their actions have a positive or negative outcome, which leads to an inability to choose between possible courses of action (other than by random selection) or to simply list all the events that may come to mind (Dehaene and Changeux, 1995). Clearly a disruption has occurred in these patients' ability to identify relational properties between their own actions and their results.

Language (again)

There is a growing agreement among neuroscientists regarding the plastic, distributed, heterogeneous, and experience-dependent character of language processes (Brown and Hagoort, 1999). Genetic factors are seen merely to correspond to general constraints on brain structure and on the timing of developmental events. These constraints are in turn regarded, to a certain extent, as accounting for the standard, classical perisylvian neural arrangement of language processing. The brain structures in this standard arrangement (especially Broca's and Wernicke's areas) are considered to be not the genetically determined components of a language-specific system. Rather, due to their cytoarchitecture, response properties, location, and connectivity, these areas are biased toward modes of processing that are suited to subserve different attributes of linguistic items (Bates, 1999; see also Damasio et al., 1996), given the contextual linkages of these items and the learning strategies associated with them. Electrical stimulation and brain imaging studies show, for example, that activity in Broca's and Wernicke's areas is most predominantly associated with sensorimotor aspects of language function — in agreement with these areas' connections with primary motor and auditory areas (Deacon, 1997). Furthermore, Broca's area has been shown to encode the goal of observed and imitative action, including motor elements involved in human conversation (Iacoboni, 2005).

The classical language areas are part of a much more widely distributed and hierarchically organized language system coordinated by the executive and recoding activity of the lateral PFC. Presumably, the lateral PFC exploits properties of the perisylvian areas to gain a processing advantage for analyzing speech. The neural architecture of language extends, however, beyond the lateral PFC, Broca's, and Wernicke's areas. Evidence from electrical stimulation and brain imaging studies shows that a number of language tasks (verbal memory, word list generation, lexical retrieval) involve activity in parietal and temporal regions (for a review, see Deacon, 1997). Deacon has suggested that language-related activity spread across different brain areas reflects those areas' specific contribution to the meaning of words (and other symbols) as relational linkages between them are retrieved (or created) and integrated (in short-term memory). Retrieval of information from those areas indeed appears to require excitatory modulation from the PFC. This is supported by a diminution of evoked potentials to sensory stimuli in posterior cortical areas reported in patients with prefrontal damage who also present deficits in focused and sustained attention (Fuster, 2001).

Theory of mind

As noted above, ToM is the symbolic extension of intention attribution/sharing. ToM functions can be neatly mapped into the three prefrontal subdivisions: lateral, orbital, and medial PFC (Lieberman, 2007), lending further support to the functional parcellation of the PFC referred to above. The lateral PFC is involved in dealing with externally focused ToM tasks. These tasks, mostly clustered in inferior PFC, include non-mentalizing aspects of ToM such as dispositional attribution, visual self-recognition, perceptual-based reappraisal, labeling of affect in facial expressions, and social and moral reasoning. By contrast, the medial orbital PFC and dorsomedial PFC instantiate internally focused tasks, having to do with emotion and motivation, respectively. Orbital PFC sustains tasks having to do with reappraisals, reflected appraisals, empathy (see below), fairness, and trust. Dorsomedial PFC is the canonical area for ToM. It activates in response to mentalizing, that is, explicit thinking or "theorizing" about the internal mental, that is, intentional states of others. Other ToM processes associated with the medial

PFC activity include processing of attitudes, autobiographical memory, self-knowledge, and dispositional attribution.

Relational action-level imitation

We suggest that the ability to imitate actions at any level of detail becomes possible when the segmentation of behavior afforded by the action recognition system becomes the object of recoding processes that allow the identification of relational properties between the building blocks of behavior, goals, and the appraisal of performance. The result is the rational understanding of action. Relational regularities found at one level can be further recoded at increasing (or decreasing) levels of detail. Neurally, relational action-level imitation can be expected to occur when the action recognition system is subsumed into the recoding activity of the PFC. All three components of the action recognition system as instantiated in the human brain (BA 44, inferior parietal lobe, and STS) have in fact been shown to mediate imitation of simple, goal-directed movements (Iacoboni, 2005; Rizzolati and Craighero, 2004). However, the activity and relationship of the action recognition system with the PFC in the context of observation and imitation of complex sequences of behaviors remains to be characterized.

Sharing of emotions and empathy

A final fundamental aspect of shared experience is the sharing of emotions and the recognition of other's emotional states as different from one's own. Brain imaging studies have shown that the first of these capacities, the more basic of the two, recruits the activity of the dorsal anterior cingulate cortex and the anterior insula (Wicker et al., 2003; Singer et al., 2004). The anterior insula, known to be connected with inferior frontal, posterior parietal, and posterior temporal cortex as well as with the limbic system, seems to play a particularly important role not only in action-driven recognition of emotions but also in their imitation. Carr et al. (2003) found evidence that the action representation circuit modulates limbic areas through the insula. They observed increased activity of insula and amygdala during imitation of emotional facial expressions. In addition to anterior cingulate and insular cortices, medial PFC and medial parietal cortex are involved when subjects perform more complex cognitive tasks (judgments) about the emotional states of others (Farrow et al., 2001). Empathy, in turn, requires not only the ability to evoke other people's feelings but also the capacity to distinguish these from one's own. Botvinick et al. (2005) reported increased activation in the VMPFC cortex when observing another person's pain but not when experiencing pain oneself, which makes of it a prime candidate for an empathy mechanism (Lieberman, 2007).

Culture in the brain: how culture influences brain function

Having considered the problem of which cognitive and neural mechanisms enable individuals to spin the shared webs of meaning that constitute culture, we now turn to a problem issuing from the fact that individuals are born into existing webs of meaning and are caught in them. This problem has to do with specific ways in which these webs manifest in particular brains. The body of research we review below evidences the great diversity of ways in which the brain adapts to the stream of cultural activity it is exposed to.

Expertise carves the brain

In an important sense, culture can be conceived as a form of expertise. This conception of culture is implied in Goodenough's definition of the concept as "whatever it is one has to know or believe in order to operate in a manner acceptable to [society's] members" (1957, p. 167). Lacking cultural expertise will reflect in a failure or difficulty to "operate in a manner acceptable" to others, in a way, that is, that renders activity mutually intelligible. It is also possible to talk about cultural experts (from shamans, to musicians, to cognitive neuroscientists), who, by virtue of a special training regime and the possession of the right social capital, have the proficiency and authority to deploy their knowledge and skills in socially appropriate contexts. The question that emerges here is how cultural expertise is acquired. Recent studies on the neuroscience of motor and cognitive skill acquisition can help elucidate the ways in which particular individuals attain greater degrees of expertise.

Karni et al. (1998) investigated the effects of training a motor task on the functional organization of the brain. Participants were trained on a finger-tapping sequence they had to practice for several weeks. The results of the experiment showed that, together with improved performance, the brain region within the primary motor cortex active during the task (M1) was larger than the area responsive for an untrained task, and remained larger weeks after participants stopped practicing. More strikingly, Bangert and Schlaug (2006) demonstrated that long-term neuroanatomical differences resulting from experience can be detected by coarse visual inspection. They showed that the characteristic omega- or knob-shaped region of the precentral gyrus associated with hand movement representation was more pronounced in professional musicians compared to nonmusicians. Moreover, the researchers found that in string players. the protrusion was more pronounced in the right hemisphere, whereas in pianists it was more prominent in the left hemisphere, indicating a link between features of neuroanatomy and acquired sensorimotor skills.

A final example of the neural manifestation of expertise in a cognitively complex activity includes differences in strategies employed by master versus amateur chess players evidenced by recruitment of distinct brain regions (Amidzic et al., 2001). This study measured electrical activity in the brain of grandmasters and amateurs while they played chess against a computer. The results of the experiment showed that in amateurs, the medial temporal lobe and hippocampus was more active. By comparison, the grandmasters' brains exhibited more activity in their frontal and parietal cortices. The reliance of the amateur players on the medial temporal lobe was interpreted as revealing a cognitive strategy that relies on the analysis of unknown moves and the initial formation of long-term memories. The strategy used by the grandmasters, on the other hand, was identified as corresponding to the usage of a memory bank of already known arrangements, problems, and solutions — a finding consistent with the involvement of the frontal and parietal cortices.

Cultural cognitive style

Differences in the systems of beliefs and values between what can broadly and loosely be labeled East Asian and Western cultural cognitive styles have been one of the foci of attention of the first wave of research in cultural neuroscience. The East Asian framework has been characterized as being holistic, relational, context-dependent, and collectivistic, while the Western framework is regarded as analytic, context-independent, and individualistic (Nisbett et al., 2001). While this dichotomy has been widely criticized, we think that, considered with a critical attitude, it still has the potential of yielding important insights into the question of how culture influences brain function. Brain activity differences related to the individualism/collectivism distinction have been identified in the perceptual domain as well as in more complex cognitive functions such as ToM and self-knowledge.

Gutchess et al. (2006) and Goh et al. (2007) have conducted two blood oxygen level–dependent (BOLD) fMR imaging studies that explore the neural basis of a difference in the processing of visual scenes between East Asians and Westerners as reported in a number of papers (Ishii et al., 2003; Kitayama et al., 2003; Nisbett and Masuda, 2003). The reported differences consist of attentional biases to either objects or backgrounds. Westerners have been shown to pay more attention to individual objects, while East Asians appear to have an attentional bias toward backgrounds. Gutchess et al. (2006) report that Westerners exhibit greater activation in sites implicated in object processing — including the middle temporal gyrus bilaterally, the left superior parietal/angular gyrus, and the right superior temporal/supramarginal gyrus. Similarly, Goh et al. (2007) have found that compared to elderly East Asians, elderly Westerners exhibit significantly greater object adaptation response (i.e., reduced BOLD response to repeatedly presented stimuli) in an object processing area (the lateral occipital complex) than their East Asian counterparts. No activation difference was reported among the younger generation of participants from both groups. The presence of a difference among the elderly groups can be explained in terms of an expertise effect.

Cognitive style effects have also been identified for ToM and self-knowledge. A second-order false-belief task (X thinks that or Y thinks that) elicited greater BOLD activity in the right insula, the bilateral temporoparietal junction, and the right dorsomedial PFC amongst monolingual US English speakers compared to their Japanese counterparts (Kobayashi et al., 2006). The Japanese participants, in turn, exhibited greater brain activity in the right inferior and orbital frontal gyri. These patterns of activity have been interpreted as underlying different ToM styles with Japanese participants more reliant on "feeling" others' emotions and response inhibition and US English speakers integrating emotions with sensory information.

Zhu et al. (2007) have provided evidence that cultural cognitive style affects the neural representation of self and other. The authors measured the brain's metabolic activity of Westerners and Chinese participants while performing a trait-judgment task that required them to decide whether a particular adjective described themselves, their mother, or a politician. Results showed that in Westerners the ventromedial PFC responded more strongly to self-judgments than to mother-judgments. This activation difference was absent in the Chinese participants. The neural representation of self and a close other would therefore appear to be unified, or at least less differentiated, in the ventromedial PFC for the Chinese participants, presumably reflecting their collectivistic, interdependent self-construal style. Westerners' individualistic, independent style would account for the observed distinction between self and other in ventromedial PFC activity. This finding lends support to ventromedial PFC playing an important role in empathy as suggested above.

Cross-linguistic differences in brain function and structure

Earlier in this paper, we dealt at some length with the problem of the cognitive and neural mechanisms that make language possible. What about the other side of this issue, the influence of particular linguistic forms on brain structure and function? Cross-cultural comparisons provide useful insights in this regard. Paulesu et al. (2000) used positron emission tomography (PET) to examine brain activation differences in English and Italian speakers associated with discrepancies identified between the orthographies of these languages. English orthography elicited greater activation in areas associated with word retrieval — the left posterior inferior temporal region and the anterior portion of the inferior frontal gyrus. In contrast, activity in the junction between the left superior temporal gyrus and the planum temporale, an area implicated in phoneme processing, was enhanced by the Italian orthography. These results are thought to reflect the degree of consistency in the mapping of phonemes to graphemes: high in Italian and low in English.

Processing-language deficits have also been shown to differently affect people who speak different languages. Dyslexia, a learning disorder characterized by a difficulty with reading, manifests in English speakers as a dysfunction of left temporoparietal cortex and inferior frontal gyrus (Shaywitz et al., 1998; Temple et al., 2003). Among Chinese speakers, in contrast, dyslexia is associated with dysfunction of the middle frontal gyrus (Siok et al., 2004). In addition to this, reduced gray-matter volume has been reported in the left parietal region for English dyslexic children (Hoeft et al., 2007) and in the left middle frontal gyrus for Chinese children with reading problems (Siok et al., 2008). These results have been interpreted as reflecting different processing demands of alphabetic versus nonalphabetic writing systems.

Cultural preferences

Behavioral evidence suggests that culture modulates underlying preference mechanisms (McClure et al., 2004). Two studies have investigated the forms these influences manifest in the brain. Erk et al. (2002) have provided evidence suggesting that human-made objects with attached cultural significance elicit activation in reward-related areas. Erk and colleagues found greater activity in the ventral striatum, orbitofrontal cortex, and anterior cingulate in response to sport cars as compared to other cars with lowered social status attached. These areas have been associated with reward and reinforcement functions. The authors suggest that activity in these regions reflect the potential social reward attached to the stimuli. McClure et al. (2004) showed that the dorsolateral PFC was affected by a cultural bias on preferences related to familiar drinks. The research team was able to show that knowledge of a culturally significant brand of soft drink significantly influenced the metabolic activity of dorsolateral PFC. More specifically, greater dorsolateral PFC activity was observed when subjects were informed in advance that they were to taste the soft drink than when this information was omitted. These results indicate that cultural regularities exert their influence by means of explicit cognitive control.

Political ideology

Political attitudes have also been shown to be associated with biases in a number of neural mechanisms. Amodio et al. (2007) found a neural basis for the reported differences in cognitive style between liberals and conservatives in the United States. They observed enhanced electrical activity in the ACC associated to the conflict generated by the change of a habitual response. Greater ACC activity was observed in liberals who were more sensitive to the change of the habitual response. In a separate study, Westen et al. (2006) investigated a different form of response conflict manifest in political judgments. Irrespective of their political affiliation, respondents in this study were less likely to acknowledge statements to be contradictory if these statements were attributed to the candidate of the same affiliation as themselves. The areas that showed greater metabolic activity when respondents failed to acknowledge the contradictions were the left insula, lateral orbital frontal cortex, and the ventromedial PFC. These activations suggest that a form of reasoning is at work that is biased to implicitly generate conclusions that are affectively preferable. This form of reasoning also suppresses adverse conclusions when individuals are faced with threatening information regarding emotion-laden expectations. In contrast to the study by McClure et al. (2004) described above, this study suggests that cultural regularities can also implicitly modulate the emotional regulation of reasoning.

Religious practices

Research in the area of religious practices has focused on those aspects of religious phenomena associated with intense, transcendental, and/or out-of-the-ordinary subjective experiences that can be said to be mediated by altered states of consciousness. The available literature shows that these experiences have a heterogeneous neural basis: different religious practices have been shown to be associated with different patterns of distributed brain activity. The temporal lobes, for example, have been implicated in several forms of religious experiences such as hyper-religiosity (Waxman and Geschwind, 1975), sensed-presence (variously reported as God, Allah, an angel, or a spirit; Persinger and Healey, 2002), and the experience of wholeness, timelessness, and unity with the universe so fundamental to many (if not all) religions (d'Aquili and Newberg, 1998). In addition, a pattern of increased metabolic activity in the frontal lobes and reduced metabolic activity in the parietal lobes has been reported for focused attention-based meditation (as manifest in Buddhist meditation, Newberg et al., 2001, and meditative praying among Franciscan nuns, Newberg et al., 2003). Frontal lobe activity has been suggested to reflect the attention-focusing component of meditation and praying, while the parietal deactivation, in turn, has been interpreted as being associated with an altered experience of self, in consonance with the parietal cortex role in visual–spatial and temporal processing as well as body orientation.

Concluding remarks

In this paper, we have reviewed studies that suggest that the shared webs of signification that make up culture are primarily the product of the activity of the PFC. This activity can be characterized as the process that renders input intelligible by recoding it into higher-order elements through a recoding function or solution that captures the relational properties of the input. Intersubjective understanding and symbolic reference, the two abilities identified in anthropology to underpin culture, are derived forms of relational recoding applied iteratively at higher and higher levels of complexity. By complexity we mean a larger number of elements (goals, then plans, then intentions, and, finally, symbols referring to these and other items), greater levels of hierarchical depth, and a less local, wider, and sparser distribution of regularities. Relational recoding corresponds to a form of inference that works by putting into context an event or object of interest, that is, by recognizing its linkages to other relevant events or objects. This form of inference can be identified as abduction. From the above discussion, it follows that intersubjective understanding and symbolic reference are applications of abductive inference. Abduction can, therefore, be regarded as the inferential engine at the heart of enculturation.

During interaction, abduction allows each interactor to form a mental model of the intentions and emotions of the other, thus forming a shared framework of thought, by making use of information that is relevant to that framework. Thus, interactors generate a shared context that makes it possible for them to understand each other. It is the context of activity that reduces the space of inferential possibilities to those that are more likely. The generation of the shared framework of thought is open to contestation owing to the divinatory character of abduction. Abduction remains a guess pending confirmation, which, as Popper (1959) showed, can never be done conclusively.

Relational recoding (and therefore abduction) appears to be instantiated in the PFC in a heterogenous manner, owing to a segregation of activity of the PFC along two dimensions: modality and context. With respect to modality, relational recoding seems to vary in a lateral-to-ventral direction with sensorimotor recoding taking place in the lateral PFC, emotional recoding in the orbital and ventromedial PFC, and motivational recoding in the dorsomedial PFC. Regarding the context dimension, recoding is proposed to vary in a posterior-to-anterior fashion, from recoding of immediate sensorimotor context in posterior PFC, to pending episodic context in polar PFC.

We should note that associative and mimetic mechanisms of enculturation are still regarded to be in operation in modern humans and, in fact, they provide the raw materials for relational recoding (cf. Deacon, 1997). In this regard, the action recognition system (made up of BA 44, inferior parietal lobule, and STS) should be expected to play an important role in enculturation.

The complement to the question of the neural and cognitive mechanisms of enculturation is how specific cultural meanings and practices are manifested in the brain. The studies reviewed in the section Culture in the brain show that the answer to this question is variegated. Perhaps the most salient finding is the extent and breadth of the influence of culture on the brain: literally all brain areas, including subcortical and cortical (and amongst the latter the PFC itself), can be said to respond to regularities in the cultural stream of experience. A second remarkable finding is that culture has both a modulatory and a constitutional influence on the brain, that is, it not only shapes preexisting patterns of neural activity but also determines whether a pattern is at all present (Han and Northoff, 2008). Also extraordinary is the fact that culture not only affects brain function (both in terms of the network of structures recruited for a task and also in terms of level of activity), but can actually change the structure of the brain, even macroscopically. The review finally reveals that cultural regularities can modulate cognitive function implicitly and explicitly (through orbital/ventromedial PFC and dorsolateral PFC, respectively). Overall, therefore, the PFC establishes relationships between things and events represented in the different areas distributed across the brain. These areas become, in this manner, more readily available for modulation or constitution by (cultural) experience. However, the PFC is the structure that stands first to be modified or constituted by cultural experience as it is the structure that lays culture's foundations.

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SECTION II

Cultural Neuroscience of Attention and Perception

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CHAPTER 5

Cultural constraints on music perception and cognition

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Abstract: Research suggests that music, like language, is both a biological predisposition and a cultural universal. While humans naturally attend to and process many of the psychophysical cues present in musical information, there is a great — and often culture-specific — diversity of musical practices differentiated in part by form, timbre, pitch, rhythm, and other structural elements. Musical interactions situated within a given cultural context begin to influence human responses to music as early as one year of age. Despite the world's diversity of musical cultures, the majority of research in cognitive psychology and the cognitive neuroscience of music has been conducted on subjects and stimuli from Western music cultures. From the standpoint of cognitive neuroscience, identification of fundamental cognitive and neurological processes associated with music requires ascertaining that such processes are demonstrated by listeners from a broad range of cultural backgrounds and in relation to various musics across cultural traditions. This chapter will review current research regarding the role of enculturation in music perception and cognition and the degree to which cultural influences are reflected in brain function. Exploring music cognition from the standpoint of culture will lead to a better understanding of the core processes underlying perception and how those processes give rise to the world's diversity of music forms and expressions.

Keywords: cross-cultural music; enculturation; music learning; memory

> Music is the universal language of mankind
> (Longfellow, 1865, p. 202)
>
> Music takes as many forms as culture
> (Cross, 2008, p. 2)

Constructs such as language, rituals, and belief systems often serve as delineators of cultural groups, functioning to identify who is an insider and who is an outsider, culturally speaking. Music, on the other hand, is often thought of — and even promoted — as a both an accessible path into a culture and a source of commonality across cultures. While this notion of music as a "universal language" has been largely discredited (Campbell, 1997; Nettl, 2001; Wachsmann, 1971), it is easy to ascertain how it gained popular acceptance.

First, music as a phenomenon can reasonably be argued to be universal. It is present in some form in virtually every society and evidence of its existence appears to stretch back well before recorded history. Second, the non-universality of any specific music is not readily apparent.

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The more propositional nature of language leads to reasonably clear determinations of that which is understood (or understandable) and that which is not. The more indeterminate "meaning" of musical sounds — apart from specific associations or other cultural references — can lead to misunderstanding, misinterpretation, and mistranslation, though these inaccuracies are rarely as evident or consequential as those involving language. Indeed, Cross (2007) proposes that music's "floating intentionality" may be at the very heart of its evolution within the human species, "affording conceptual and social spaces within which individual and collective imaginings can take place" (p. 157). In other words, music's ability to accommodate multiple interpretations may have facilitated negotiation among early human societies. Third, a small number of music styles and genres have gained popularity (or at least visibility) throughout many of the world's societies. The ubiquity of Western classical and popular music across the world may lead one to presume a global commonality of musical taste and experience.

Coupled with these observations is the arguably limited generalizability of current cognitive models of music processing. Much of the research literature investigating processes of musical development and music cognition reports data collected from a culturally limited range of participants, typically individuals encultured in Western or, to a lesser extent, Asian societies. Likewise much of the material used in music research to date predominately includes either music from a limited collection of traditions (largely Western art music) or musical stimuli pared down to isolate some specific parameter (e.g., duration, frequency) to the extent that any particular cultural association is removed. While the conclusions of these studies may be valid across a variety of musical interactions, it is only through comparative study of a broad array of music traditions and listeners that we can begin to develop more generalizable conclusions about human musical thinking.

In this chapter we will consider several ways in which culture has been approached as a variable in the study of music perception and cognition, with particular attention paid to recent neurological investigations of musical interactions. We will examine the process of music enculturation beginning from fundamental categorization of music stimuli through increasingly complex music processing challenges, including an overview of our own research on the influence of culture in musical memory. We conclude by proposing some promising areas for future study.

Foundations of music enculturation

While constructs such as pitch and duration serve as fundamental components of music, it would be unlikely that any given isolated instance of pitch or duration could be characterized as culturally grounded. Culture-specific practice begins to emerge in the relationships among these basic units and the degree to which such relationships are considered typical, acceptable, or desirable. It is this very typicality that underlies current theories of development which posit that individuals use a process of "statistical learning" to generate rule structures including those that govern interactions with music (McMullen and Saffran, 2004; Saffran et al., 1999). Fundamental features that distinguish one music culture from another include the pitch collections from which melodic material is derived (scales) and the strong/weak pulse patterns over which duration is organized (meter). General sensitivity to pitch and metric features is evident early in infancy. Infants can discriminate relevant musical features without regard to cultural boundaries up to about 10 months of age. After that point, Western children begin to respond differentially to musical structures from their home culture compared to culturally unfamiliar scales or meters (Hannon and Trehub, 2005a; Hannon and Trainor, 2007).

Responses to pitch structures

A series of studies by Lynch and colleagues (Lynch et al., 1990, 1991; Lynch and Eilers, 1991, 1992) explored the influence of cultural background on the perception of mistuned notes in major, minor, augmented, and Javanese *pelog* scales. They found a clear benefit (lower discrimination thresholds) for culturally familiar stimuli (major and minor scales) among children and adults though perceptual acuity differed by both age and training. In two studies employing infants (Lynch et al., 1990; Lynch and Eilers, 1992) they found that enculturation effects emerged most clearly after one year of age.

Hannon and Trainor (2007) speculated that enculturation is a bottom-up process in which culture-specific music knowledge is built upon more general sensitivities to pattern and categorization. Further, they observed that sensitivity to more culturally specific characteristics (harmonic structure) appears to follow sensitivity to more broadly applicable characteristics (key membership). As an illustration, Neuhaus (2003) reported use of both general listening strategies (categorical perception, pattern detection) and culture-specific responses among Turkish, German, and Indian musicians when listening to a variety of familiar and unfamiliar scale patterns. The participants demonstrated common differential ERP responses — P300 as well as a late-occurring (430 ms+) general negative shift — that reflected expectancy violations relative to their own music systems but not in response to violations within culturally unfamiliar systems.

Differences in musical responses observed between cultural groups may reflect differences in the ways in which individuals interact with music in a given society. When compared to English-speaking Canadian children, Japanese 5 and 6 year olds demonstrated greater proficiency recognizing original versus pitch-shifted versions of familiar melodies (Trehub et al., 2008). Trehub and colleagues argued that an emphasis on pitch labeling characteristic of music teaching in Japanese schools could have facilitated more robust processing of tonal stimuli thus resulting in a greater sensitivity to deviations from known melodic material.

It is interesting to note that children with more advanced second language production skills are more successful at discriminating non-native phonemes as well as fine mistunings of a major triad (Milovanov et al., 2008). As individuals with more sophisticated language skills are required to re-categorize phonemic units according to new rule systems, one might speculate that a similar degree of sensitivity is required to interpret culturally unfamiliar music on its own terms. Future work may examine whether advanced second language skills could facilitate more authentic (more like that of a cultural insider) processing of music built using unfamiliar pitch constructions.

Response to rhythmic structures

Organization of rhythmic material may also reflect the influence of enculturation. In a study of cross-cultural rhythm perception, Hannon and Trehub (2005a) found that, unlike adults, 6-month-old infants were equally adept at recognizing rhythmic violations in culturally familiar (Western) and unfamiliar (Balkan) metric contexts. A subsequent study (Hannon and Trehub, 2005b) found that North American infants as young as 12 months of age began to demonstrate less sensitivity to disruptions of unfamiliar non-isochronous metric patterns (varied durations between pulses) typical of Balkan folk music while maintaining sensitivity to familiar isochronous metric patterns (equal durations between pulses) typical of North American folk music. These changes in sensitivity based on cultural norms are similar to age-related changes in responses to pitch structures and linguistic information. However, after a brief period of repeated informal exposure to unfamiliar metric patterns, researchers were able to reverse the effects of enculturation and older infants' responses to non-isochronous examples were virtually identical to their responses to isochronous examples. In contrast, adults showed some improvement in their responses after exposure but to a much more limited extent.

When tapping along with a selection of French and Tunisian popular songs, French and Tunisian adults tapped to hierarchically more complex levels of rhythmic organization among selections that were more culturally familiar (Drake and Ben El Heni, 2003). This finding is consistent with earlier single-culture studies demonstrating that access to rhythmic complexity in tapping is indicative of greater musical expertise (Drake et al., 2000a, b). The degree to which rhythm is a prominent organizational feature of one's most familiar music style may also influence the way in which he or she interprets not only rhythmic material, but melodic complexity as well (Eerola et al., 2006). Even such seemingly basic points of interpretation as location of a downbeat appear dependent on encultured knowledge (Stobart and Cross, 2000).

Suggesting that rhythmic grouping might correspond to language accent patterns, Iversen et al. (2008) reported that English speakers tended to organize metric patterns into short-long groupings, while Japanese speakers exhibited greater variability in their responses though most often preferring long-short groupings. Similar relationships between linguistic and musical rhythm patterns have been observed even in comparisons of the instrumental music of French and English composers (Patel and Daniele, 2003). It is not yet possible to speculate whether characteristics of one mode of expression influences the other or whether each reflects deeper domain-general but culture-specific organizational principles. However, future research could explore the nature and generalizability of these findings that suggest an intriguing approach to the influence of culture across domains.

Interacting with complex musical structures

While the ability to discriminate, categorize, and consolidate discrete aspects of musical information is arguably a prerequisite for musical understanding, most interactions with music involve the processing of constructions that are complex, large-scale (at least compared to isolated tone sequences or patterns), and laden with associations. Moreover, interactions with complex musical structures lead not only to the "figuring out" of a song's organizational principles, but also to such comprehensive outcomes as affective response and retention in memory. For our purposes here we will specifically address individuals' responses to musical sounds themselves rather than to cultural associations or culture-specific social practices in which music features prominently. Admittedly it is likely impossible to parse an individual's encounter with music so neatly.

Scalar and metric structures, among others, provide frameworks upon which musical information can be superimposed and organized. It is the virtually infinite variety of that musical information that gives rise to the vast repertoires within any given music tradition. For example, a task as simple as recognizing the boundaries of a musical phrase requires individuals to draw on a combination of encultured principles of pitch hierarchy, contour, metric patterning, and rhythmic organization of sound and silence. Though both German and Chinese listeners demonstrated similar ERP responses associated with phrase closure for Western and Chinese melodies, both music style and listener culture significantly affected averaged responses early in the time course (100–450 ms) (Nan et al., 2006). In a subsequent study using functional imaging, musically trained German listeners completing a style categorization task demonstrated a right-lateralized network of activation associated only with listening to culturally unfamiliar Chinese melodies (Nan et al., 2008). Activated areas included right middle frontal and inferior parietal regions along with the right posterior insula. Results were interpreted as reflecting increased cognitive and attentional demands associated with the unfamiliar style.

Right-lateralized activity has also been reported among Western listeners in conjunction with melodic rule violations. Out-of-key melodic material evoked early right-lateralized negativities while memory-only violation evoked left-lateralized N400 responses (Miranda and Ullman, 2007). This is consistent with models that implicate right anterior-frontal areas in musical prediction among both adults as well as 10-year-old children (Koelsch et al., 2005; Koelsch, 2009).

When responding to structured versus unstructured melodies, both trained and untrained listeners demonstrated stronger bilateral activation of the inferior frontal gyrus, anterior STG, and premotor cortex along with right-lateralized activation of posterior STG (Minati et al., 2008).

ERP data showed a frontward shift of N2 response for structured melodies indicating activity in areas associated with classification and categorization, possibly reflecting the clearer organizational structure of these melodies.

Levitin and Menon suggest that such bilateral frontal activation may reflect the organization of information across time. They reported significant activation of left (and to a lesser extent right) inferior frontal areas among musically untrained Western adults when listening to intact (temporally organized) as opposed to scrambled (temporally unorganized) selections of Western classical repertoire (Levitin and Menon, 2003, 2005). Interestingly, both Levitin and Minati employed comparisons of organized and disorganized musical material. In contrast, comparing responses to music from different cultures reflects a comparison between organized and "differently organized" music. The latter distinction may result in much more subtle differences in both behavioral and neurological responses to music.

Perhaps the broadest aspect of complex music processing is affective response. Japanese listeners with varying levels of formal musical training successfully distinguished Japanese, Western, and Hindustani instrumental performances intended to convey joyful, sad, or angry emotions (Balkwill et al., 2004). Using a similar forced choice design, Fritz et al. (2009) reported that Western and African (Mafa) adult listeners recognized Western music examples characterized as happy, sad or scared/fearful. European and Indian listeners demonstrated less agreement selecting adjectives to describe a series of Western, Indian, and New Age examples (Gregory and Varney, 1996). However, when asked to identify the correct descriptive titles for New Age examples, both groups of listeners responded similarly. Sensitivity to affective content does not appear to be independent of sensitivity to technical aspects of the performance ranging from such broad constructs as loudness or tempo (Balkwill and Thompson, 1999) and mode (Fritz et al., 2009) to more subtle nuances like use of portamento or tenuto (Adachi et al., 2004). Wong and colleagues (in press) reported that adult listeners born in the United States gave higher ratings of tension to examples of Indian music; likewise, listeners born and raised in Bihar, India rated examples of Western art music as more tense. It is notable that the greatest degree of agreement between different listener groups was reported in cases in which the task was one of identifying the affective intent of a performance and the number of possible responses was small. Less inter-group agreement was apparent in cases where listeners were asked to report their own affective responses.

Given the difficulty of ascribing specific, declarative meaning to music, how can one identify conditions under which musical utterances are "misunderstood" from a cultural standpoint? Morrison, Demorest, and colleagues rationalized that listeners encountering music constructed according to familiar rules and conventions would be likely to process it more robustly, retaining not only the surface information presented (e.g., instruments, tempo) but the deeper forms and structures of the performance (Demorest and Morrison, 2003). In other words, listeners may more successfully get the "gist" of culturally familiar music than that which is unfamiliar (Agres and Krumhansl, 2008), thereby leading to better encoding and recall of what was heard.

Culture and musical memory

In a recent series of studies we have used memory for novel music examples to examine interactions with culturally familiar and unfamiliar music (Demorest et al., 2008, in press; Morrison et al., 2003, 2008). In an fMRI study involving US-born adult musical novices and highly trained professional performers, participants listened to a series of 30 s Western classical and Chinese classical music examples while undergoing a functional scan. Following the scan, participants identified a series of short (4–8 s) music excerpts as either taken from or not taken from the longer examples. Both groups demonstrated more success recognizing previously heard Western examples even though none of the specific selections used were familiar to the participants.

We had hypothesized that listening to culturally familiar music would produce greater levels of brain activation analogous to those demonstrated when listening to a familiar language (Schlosser et al., 1998). However, while behavioral responses (the recall test) showed a clear distinction between the two music types, scanning data did not reveal any activation unique to culturally familiar music listening.

To substantiate the behavioral findings, we conducted a more extensive music memory test employing musical examples from three cultures and 150 adult subjects born in the United States and Turkey both with and without formal music training (Demorest et al., 2008). Again participants demonstrated significantly better memory performance for novel examples taken from their own culture (Western or Turkish classical) than from an unfamiliar culture (Chinese classical). Participants' level of formal music training had no effect on their success at this task. Interestingly, Turkish listeners — who presumably encountered Western music styles on a regular basis and, in the case of the Turkish music conservatory students, formally studied Western classical music as part of their curriculum — demonstrated responses to the Western music examples that, while more accurate than for Chinese music, were significantly less accurate than responses to Turkish music (Fig. 1).

In a follow-up study (Morrison et al., 2008), a similar test was administered to US-born adults and fifth-grade elementary school students (approximately 10–11 years of age) using Western and Turkish music examples of varied complexity. Regardless of age or music complexity, participants were again more successful remembering culturally familiar music, suggesting that certain cognitive boundaries are set in place early in life. This generalized the earlier findings to a much younger age group, but also to a qualitatively different set of stimuli. While the earlier studies had used ensemble music of some complexity, the simple condition of this study involved performance of a single instrument and featured examples with a relatively high degree of motivic redundancy. For these simpler examples to be sensitive to cultural associations suggests that cultural knowledge may influence music processing at a fairly fundamental level.

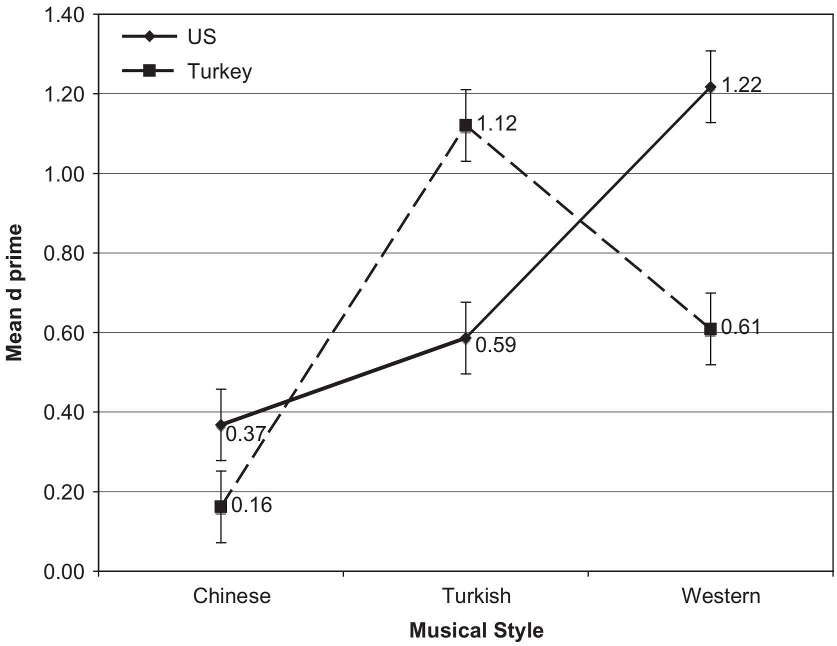

Fig. 1. Mean d-prime scores for adult listeners from the United States and Turkey demonstrate most accurate recall for culturally familiar music (Western and Turkish classical, respectively).

This finding, which we have dubbed an "enculturation effect", has been further replicated in a recent study of Western and Indian adults (Wong et al., in press) allowing generalization to a still broader range of both listeners and styles. Turkish subjects in the earlier study demonstrated better performance for music to which they had limited exposure (Western) versus no exposure (Chinese). To test the effects of concentrated exposure, we conducted a study to determine if the effects of enculturation on memory could be mediated among elementary aged children through focused instruction. We found that even after an extensive and immersive 8-week curricular unit focusing on Turkish music traditions, fifth-grade students failed to demonstrate significant improvement in their memory for Turkish music as compared to Western (Morrison et al., 2009).

Having amassed strong evidence for culture-based differences in music memory, it remained to be examined how this behavioral difference might be reflected in neurological activity. Having observed no pattern of activation unique to culturally familiar music (Morrison et al., 2003), we speculated that this lack of difference might be due to listeners' employment of identical cognitive strategies — strategies learned through informal learning — regardless of the music they encountered. In other words, perhaps individuals drew on encultured processing approaches in an effort to "accommodate" unfamiliar music material (Demorest and Morrison, 2003). If so, then one might expect to observe evidence of the greater cognitive load presumably necessitated by the awkward and unfamiliar (from the listener's perspective) music constructions. Increased frontal activity would be consistent with results reported for German musicians categorizing a series of culturally unfamiliar Chinese melodies (Nan et al., 2008) and may reflect increased processing difficulty (Baker et al., 2001). In a related finding that appears to support this supposition, Tillmann et al. (2003) reported that related and unrelated harmonic targets resulted in bilateral inferior frontal activation among adult listeners, with the unrelated targets giving rise to stronger activation.

To test this hypothesis we sampled 16 US and Turkish born subjects with limited formal musical training (Demorest et al., in press). Using fMRI procedures we scanned subjects during two tasks: (1) listening to novel musical examples from their own culture (Western or Turkish classical music) and an unfamiliar culture (Chinese traditional music); (2) identifying which among a series of brief excerpts were taken from the longer examples. Again, behavioral results demonstrated better memory for the culturally familiar music styles. Difference maps showing areas of greater activation during listening to unfamiliar music than familiar music displayed significant activation of the left cerebellar region, right angular gyrus, posterior precuneus, and right middle frontal area extending into the inferior frontal cortex for all subjects (Fig. 2a). For the memory task,

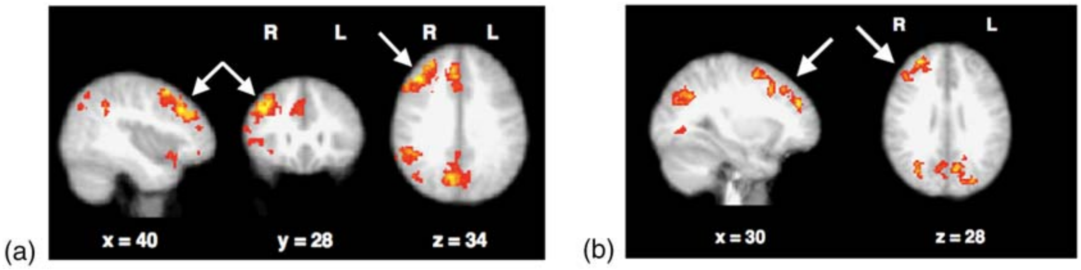

Fig. 2. Difference map showing (a) areas of greater activation during listening to culturally unfamiliar music in R angular gyrus (AG), paracingulate gyrus (PG), posterior precuneus (PC), and middle frontal areas extending into the inferior frontal cortex (FC) for all subjects; (b) for Western subjects listening to Turkish music greater activation of the PC and R middle frontal gyrus (FG); activation in the R AG and PG is shown though it did not reach cluster significance; for purposes of comparison, coordinates displayed correspond to those shown in (a).

comparing unfamiliar to familiar music revealed significant activation in the cingulate gyrus and right lingual gyrus. To test the findings further we compared Western listeners' responses to Turkish music, a second unfamiliar culture. As with the Chinese examples, Western listeners demonstrated significant activation of the precuneus and right middle frontal gyrus when listening to Turkish music contrasted to listening to Western music (Fig. 2b). In all cases, direct comparison of Western and Turkish subjects' difference maps revealed no significant activation unique to either group.

By selecting music memory as a measure of music comprehension we may have chosen a process that is particularly slow to respond to unfamiliar music systems. Other more specific tasks such as familiarization with alternate scale structures (Castellano et al., 1984) might be mastered more quickly as a result of practice or guided learning. Neurological evidence of learning might be observed earlier still. Within the first 14 h of second-language (L2) instruction learners demonstrated characteristic N400 responses to L2 words and pseudowords; they did not demonstrate overt discrimination ability until after over 60 h of instruction (McLaughlin et al., 2004). The application of similar research designs to musical interactions may reveal much about the way in which individuals gain knowledge of unfamiliar musical systems.

Future directions

Research has considered cultural boundaries of music processing at various levels of complexity. However, the interrelationship among these levels remains to be determined. It is possible that the difficulty individuals demonstrate remembering culturally unfamiliar music may be due to an inability to accurately and efficiently parse phrase boundaries that may, in turn, reflect a lack of facility with culturally specific systems and hierarchies of pitch or meter. It will be useful for future research to examine how specific aspects of music may contribute to the broader ability to apply familiar organizational and "sense-making" processes to it.

Recent evidence suggests that, over an extended period of early and largely informal listening experiences, individuals can develop familiarity with multiple cultural traditions (e.g., Western and Indian art music) such that both memory and affective responses are no different than those of native listeners, a phenomenon referred to as "bimusicality" or "bimusicalism" (Wong et al., in press). In contrast, other research reports better memory for culturally familiar music even among those with extensive performance study in a second music tradition (Demorest et al., 2008). The degree to which listening versus active participation, or informal versus formal training, contributes to music enculturation is a promising question for future study.

Though the application of neuroscientific research methodologies to the question of music and culture is still in its early stages, evidence suggests that neurological responses to culturally familiar and unfamiliar music appear to differ more by degree than substance, a conclusion similar to that reported for language processing (Paulesu et al., 2000). It is unlikely that individuals from different cultural backgrounds employ different systems in the processing of musical information. It is more likely that different musical systems make different cognitive demands (e.g., Eerola et al., 2006). For example, Western art music's reliance on harmony, the prominent role of melodic mode structures in North Indian *rags*, and the interaction of rhythmic timelines in the music of the Ewe each requires different balances of cognitive engagement. Among encultured listeners and performers such balances may be reflected in varied patterns and relative strengths of neurological activity analogous to differences observed among speakers of tonal and non-tonal languages (Kaan et al., 2008; Klein et al., 2001).

It is possible that, while enculturation facilitates the establishment of particular schemas through which humans process music, individuals are able to distinguish between not only what is musically familiar and unfamiliar, but what is musically likely and unlikely. Responses to culturally unfamiliar melodic (Nan et al., 2008) or metric (Hannon and Trehub, 2005a) constructions — or even complex intact performances (Demorest et al., in press) — appear to be distinct from responses to material that is merely unconventional or jumbled (Levitin and Menon, 2003; Trehub and Hannon, 2009). Perhaps humans are simply responsive to logical systems of construction even though the specific logic of a specific system may be elusive to a cultural outsider. Hannon and Trehub suggest that pattern detection and categorization are foundations from which culture-specific knowledge springs. One may speculate that listeners are able to deploy systems of pattern detection even in the absence of culture-specific knowledge that would ultimately facilitate such tasks as information parsing (Nan et al., 2008) or prediction (Huron, 2006).

On a broader scale, the question may be raised whether there are more and less delimiting dimensions to musical enculturation. Though culture is often viewed through an ethnic, societal, or geographical prism, can one also speak of an age culture? An historical culture? A philosophical culture? Would similar variability of responses be found along each of these lines of distinction? Considering the long-term nature and arguably permanent enculturation addressed by much of the research presented here, it would seem difficult to equate identity accrued over time as a member of a societal entity — for example, identity as a white Western European city-dweller — with identity adopted on a temporary basis — for example, as an independent-minded adolescent. While both identities may be equally powerful in driving one's actions and decisions regarding musical engagement, it is not known how each may contribute to cognitive processing strategies.

The salience of musical culture may also be task dependent. For example, Turkish listeners demonstrated stronger frontal responses to a familiar instrumental timbre (*ney*) than a less familiar timbre (cello) when music was presented as background to an unrelated oddball task (Arikan et al., 1999). Conversely, other findings show stronger frontal activity among Turkish listeners when encoding Chinese instrumental music (a culturally unfamiliar style) compared to Turkish instrumental music (Demorest et al., in press). Rather than isolating culture alone as a variable of interest, it will be useful to include it in studies of a variety of music-related tasks.

To return to the initial notion of music's universality, study of music and culture may shed light on how constructs of cultural generality and cultural specificity co-exist. Nettl (2001) asks, "can it be true that every musical utterance has in it intervals approximating the major second or something of that general sort?" (p. 467). Perhaps not. Rather, might it be the listener who carries with her the organizational construct of the major second, a construct with which she organizes and makes sense of the musical tradition in which she has been encultured? She might then apply this construct to increasingly distant musical encounters until its application utterly fails. In this way, we might see the notion of musical universality residing within the individual rather than in the construction of the music itself.

Cross (2008) notes that "musicality appears to be integrally bound to the human capacity for culture, not as symptom but as partial cause" (p. 14). Music itself is a practice that is shared across human societies and that gives rise to cultural distinction. It follows that music — far from being simply a cultural artifact — may be seen as a both a broad human disposition and a manifestation of culturally rooted cognitive processes.

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CHAPTER 6

Culture and attention: evidence from brain and behavior

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Abstract: Research has demonstrated that our experiences, including the culture in which we are raised, shape how we attend to and perceive the world. Behavioral studies have found that individuals raised in Western cultures tend toward analytic processing and prefer tasks emphasizing independent contexts rather than tasks emphasizing interdependent contexts. The opposite is true for individuals raised in East Asian cultures, who tend toward holistic processing and prefer tasks emphasizing interdependent contexts. Recently, cognitive neuroscientists have extended these behavioral findings to examine the brain activity of individuals from different cultures during the performance of cognitive tasks. Results from these initial studies indicate that culture may shape how the brain processes even very abstract stimuli and may influence the features of the environment to which individuals attend. The present chapter reviews evidence that culture influences attention and related systems, which, in turn, impact other cognitive and social processes and their neural correlates.

Keywords: fMRI; cultural differences; attention; holistic and analytic processing; independent and interdependent context

A basic assumption of cognitive science is that humans from all walks of life rely upon the same evolved neural architecture, but that an individual's life experiences may shape the contents of this basic structure. Recent studies, including research using neuroimaging techniques, have expanded this view, providing evidence that not only the content of cognitive and neural representations can be altered by life experience within a cultural context, but the processes likely to be engaged under certain circumstances may also be molded by acculturation over a lifetime (Han and Northoff, 2008; Nisbett et al., 2001). One particularly surprising finding to emerge from this research is that cultural ideas and practices appear to influence even processes that are seemingly universal, including processes related to perceptual, attentional, and mnemonic representations (Hedden et al., 2008; Kitayama et al., 2003; Masuda and Nisbett, 2001).

These cultural investigations have led to a generalization that cultural ideas and practices tend to encourage one of (at least) two distinct modes of processing information that greatly influence the

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aspects of the environment to which we attend (Markus and Kitayama, 1991; Nisbett et al., 2001; Triandis, 1995). Holistic processing involves a wide attentional field that responds to the context in which objects and actors are embedded and, by extension, attributes causality to situational factors. In contrast, analytic processing involves a relatively narrow but focused attentional field that concentrates primarily on distinctive objects and their features and attributes actions and intentions to objects and actors. Although this division represents a simplification of the many dimensions along which cultures may vary, these two modes of processing can roughly be described as being more predominant in some cultural contexts than in others. These predominant tendencies, instantiated in institutions and environments, may subtly encourage a given mode of thought in individuals raised within a cultural context.

There are obviously many dimensions on which cultures may differ, including access to natural resources and trading partners, geographical isolation, language, kinship structure, institutional organization, and national history. Nonetheless, differences associated with a predominance of holistic and analytic modes of processing appear to be deeply rooted in East Asian and Western cultural contexts and appear to be associated with a predominance of interdependent and independent self-construals within those cultural contexts (Markus and Kitayama, 1991). Interdependent self-construals generally are associated with a view of the self as being defined and dependent upon relationships with others, with one's position in a social hierarchy, and with the status afforded to one by externally derived criteria (such as the extent to which one is respected, agreed with, and relied on by others). Independent self-construal is typically associated with a view of the self as being defined by one's own actions and achievements rather than social position, with one's merit and intentions rather than recognition by others, and with internally motivated criteria (such as likes, desires, and beliefs).

One early and wide-ranging attempt to describe and organize the multitude of dimensions that characterize cultural value systems was made by Hofstede (1980), who described "universal" patterns that included individualism and collectivism. Also included were the dimensions of power distance, uncertainty avoidance, and masculinity versus femininity. Individualism–collectivism is a major dimension of cultural variability, explaining differences and similarities across cultures. This theoretical organization has been highly influential on later cross-cultural research in the psychological sciences. Hofstede rated each nation under study with two numerical ratings, one for the degree of individualism and one for collectivism. Especially individualistic countries are the United States, Great Britain, Canada, and Germany. Latin America, South-East Asia, and Africa tend toward a more collective form of society. Because of the number of nations studied, Hofstede's work represents what is probably the most comprehensive study on cross-national individualism and collectivism. Although such national characterizations provide a macroscopic generalization of the predominant tendencies within a nation or culture, it is important to note that within a given cultural context, certain individuals will tend more or less toward the typical characteristics of individualism or collectivism and their associated preferences in social and cognitive processing.

According to Hofstede (1980), in individualist cultural contexts, one's identity is based primarily on personal accomplishments, and there is an emphasis on personal autonomy and self-fulfillment, a focus on rights above duties, and concern for oneself and immediate family. Individualistic societies tend to be fundamentally contractual, consisting of narrow primary groups and negotiated social relations, with specific obligations and expectations for the purpose of achieving status (Schwartz, 1990). To an individualist, emotional self-expression and attaining one's personal goals are important sources of life satisfaction (Markus and Kitayama, 1991). Individualists give priority to personal goals over the goals of groups or other communal organizations (Triandis et al., 1988). In Western individualistic cultures, such as those in North America and Western Europe, it is believed that attitudes, feelings, and behaviors should be determined by the self without being controlled by an external cause (Markus and Kitayama, 1991).

Western individualism has consistently supported rights for personal freedom and enhancement (Hsu, 1985).

By contrast, collectivist cultures tend to be communal societies exemplified by diffuse and shared obligations and expectations (Schwartz, 1990). With regard to emotional expression, collectivism emphasizes social roles and obligations rather than individual goals and pursuits (Kwan et al., 1997; Markus and Kitayama, 1991). Restraint in emotional expression is valued as a means of ensuring in-group harmony. Collectivists either make no distinctions between personal and collective goals, or if they do, they subordinate their personal goals to the collective goals (Triandis et al., 1988). Chinese appear to be relatively more oriented toward significant others rather than toward the individual self (Chu, 1979). In collectivist societies, one's identity is linked with an in-group network, a network that relies upon the values of perseverance, obedience, duty, and loyalty (Hsu, 1985). People in collectivist cultures strive toward feelings of belonging to the social in-groups, interconnectedness, and seeking to maintain harmony. Exercising personal choice is often discouraged, as such actions may threaten group harmony and emphasize differences among group members (Triandis, 1995).

These different self-construals (independent and interdependent) and the social value systems affiliated with them (individualist and collectivist) influence more than a person's view of themselves — they have extensive implications for cognitive processes that help us all interact with and respond to our social and natural environments. Research has found that interdependent individuals tend to be more sensitive to the needs and emotions of others within their group than are independent individuals (Markus and Kitayama, 1991; Matsumoto, 1989) and also to in-group versus out-group status when making decisions that affect another person (Leung and Bond, 1984). In addition to such higher-level social contexts, recent studies have observed that low-level perceptual and attentional processes are also informed by these two different modes of self-construal.

Many prominent ideas and practices prevalent in American culture require separating objects from their contexts and making independent or absolute judgments. In contrast, many prominent ideas and practices in East Asian culture require connecting objects to their contexts and making interdependent or relative judgments (Nisbett et al., 2001). This divergence in what we attend to likely begins at a very young age and is present in nearly all aspects of the culture in which one is reared (Chao, 1995). These culturally derived influences pervade our life experiences, and may subtly bias us to attend to particular features of the environment. Individualist cultural contexts tend to emphasize attention to specific objects and actors, examining focal objects for distinctive features and causal relations. In contrast, collectivist cultural contexts tend to emphasize attention to the surrounding context in which objects and actors are embedded, examining the relationships between parts of a whole in order to determine the situational and contextual features that influence one another. Throughout a lifetime of subtle and not so subtle emphasis on certain aspects of the environment, we may come to learn to employ specific perceptual and attentional processes that are favored by our cultural contexts.

Behavioral studies of attention

Attentional processes guide our interactions with the world, influencing the aspects of our environment to which we orient, allow entry into memory, and promote as important causal entities in our reasoning. From the perspective of cognitive psychology, attention acts as the gateway to our internal representations. As such, the influences of culture or other life experiences on attentional processes will have important and sometimes complex consequences for other cognitive operations, including perception, memory, and reasoning.

At the level of visual perception, cultural differences in attention have been observed when participants attend to a focal object (referred to as analytic processing) as opposed to attending to the context within which an object resides (referred to as holistic processing). These tendencies can be loosely described in the context of gestalt theory (Wertheimer, 1944; Köhler, 1947), in which visual scenes are separated into the figure and the ground. Certain perceptual features, such as similarity, proximity, continuity, and closure allow multidimensional visual scenes to be distinguished into focal objects and their surrounding contextual fields. These properties influence the perception of even very simplistic and abstract visual stimuli, such as a line extending downward from the upper side of a square (see Fig. 1a). Because the line is not continuous with the square, it is usually perceived as a separate object (the figure) while the square is perceived as the surrounding context (ground).

Using such simple stimuli, Kitayama et al. (2003) asked East Asian (Japanese) and Western (American) participants to reproduce, after a brief delay, the length of the line based either on the line's size relative to the size of the framing square, or on the absolute length of the line (ignoring the size of the framing square). Japanese tended to be more accurate at reproducing the ratio of the line's length relative to the square than at reproducing the line's absolute length (i.e., regardless of the size of the square), whereas Americans showed the opposite tendency, exhibiting greater accuracy in reproducing the line's absolute length (Kitayama et al., 2003). One important finding from this study involved the inclusion of groups that were cultural immigrants (Westerners studying in Japan and Japanese studying in the United States). These groups exhibited tendencies that were more similar to their host countries than to their home countries — that is, Westerners in Japan tended to be more accurate when reproducing the length of the line relative to the square and less accurate when reproducing the absolute length of the line relative to their home-country counterparts, while Japanese in the United States were equivalent in accuracy when reproducing the relative or absolute length of the line. These results indicate that even very brief exposure to another culture (participants had resided in the host country for 2 months–4 years) may be sufficient to influence one's attentional and perceptual tendencies. Alternatively, individuals who already tend to think and behave in a manner that is more consistent with the host country than with their home country may be more likely to journey abroad for their studies.

Although potentially malleable, these cultural predilections arise at a relatively early stage of development. Duffy et al. (2009) conducted a similar study in Japanese and American children (aged 4–13 years) and observed that these cultural tendencies were present in children as young as 6 years of age. Before 6, however, children from both cultures performed similarly when making absolute and relative judgments of line lengths. These studies demonstrate that cultural influences may affect perceptual tendencies on highly abstract tasks from an early age, with East Asians tending to be more adept at integrating an object with its context and Westerners tending to be more adept at extracting a focal object from its context.

An important caveat to the Kitayama et al. (2003) results is the behavior of the Americans in the United States, who performed more accurately on the absolute judgments than on the relative judgments, a finding that is inconsistent with prior findings from the visual literature of better performance when using a reference frame (Baranski and Petrusic, 1992; Rock and Ebenholtz, 1959). This was examined in an extensive study by Zhou et al. (2008), who failed to replicate the Kitayama et al. (2003) cultural effects using substantially similar procedures with Chinese and American participants. Instead, they found that all participants, regardless of culture, judged a line's relative length more accurately than its absolute length. Although these results cast some doubt on the replicability of Kitayama's findings, it should be noted that results that did replicate the increased accuracy of Americans on absolute, as compared to relative, judgments were also observed in studies with children (Duffy et al., 2009; Vasilyeva et al., 2007). A potential explanation for the Kitayama et al. (2003) effects may be found in a nuance of the original study, in which a condition was included where the identical square was presented as a reference at the time of encoding and reproduction for both the relative and absolute instructions. In this case, participants should reproduce identical lines for both the relative and absolute instructions, and one would expect both cultures to perform similarly for these stimuli. The fact that cultural differences were observed even for these identical stimuli suggests that culture was likely not influencing perceptual processes per se, but was instead influencing factors related to the task itself (also noted by Zhou et al., 2008). One possibility is that each culture responded differentially to the task such that East Asians were more likely to focus on the framing square regardless of task instruction, while Americans were more likely to focus on the line as a distinct object — such tendencies could be explained by attention biasing the manner in which participants from each culture approached the task, rather than culture shaping the visual percepts themselves. Such a possibility is suggested by related neuroimaging results (see next section) from Hedden et al. (2008), who found regional brain differences in areas associated with attentional control, but not in perceptual regions, in a version of the task modified for use in the MRI scanner, despite the absence of cultural differences in behavior. Further research will be necessary to fully elucidate the impact of cultural context on the interaction of attention and visual perception in this and related tasks.

In a similar line of research, Ji et al. (2000) looked at cultural variation in attention and perception using the rod-and-frame test, designed by Witkin and colleagues (Witkin, 1967, Witkin and Berry, 1975; Witkin and Goodenough, 1977). This task was used to measure the influence of context on perceptual judgment. Participants viewed a rod inside of a frame that was fixed by the experimenter to various angles and were asked to independently rotate the rod to a position in which it was objectively vertical, without reference to the frame position. East Asian participants made more errors in this task than did American participants, likely because they found it more difficult to ignore the contextual influence of the frame. Ji et al. (2000) attributed these results to attentional differences between the two cultures.

A number of other studies have implicated cultural differences in attention to what is perceived and remembered about complex visual scenes (Masuda and Nisbett, 2001, 2006; Masuda et al. 2008; Miyamoto et al., 2006). Using a variant of the change blindness paradigm (Simons, 2000; Simons and Levin, 1998), in which participants are often unaware of manipulations to unattended aspects of a visual scene, Masuda and Nisbett (2006) demonstrated that East Asians (in this case Japanese) have a tendency to attend to the entire visual field and to relationships among objects in that field, whereas Americans tend to focus on the attributes of salient objects within the visual field. Japanese and American participants viewed sequential animated vignettes that differed in small details. Changes occurred either in the attributes of salient, focal objects (such as the color of the object) or in the contextual field (such as the location of background objects). Americans were more likely to detect changes in attributes of focal objects, while Japanese were more likely to detect changes in the background and in relationships among objects. In a related study, Miyamoto et al. (2006) demonstrated that these cultural tendencies may be at least partially afforded by environments characteristic of individual cultures. They selected scenes that were typical of small, medium, and large cities in both Japan and America. Typical Japanese scenes were found to be more ambiguous and complex than typical American scenes. Next, these researchers used these typical scenes as primes presented before the change blindness task used by Masuda and Nisbett (2006). Individuals (whether Japanese or American) were more likely to detect changes in the background context of sequentially presented animated vignettes when they were primed with typically Japanese scenes than when primed with typically American scenes. Although Japanese participants detected more contextual changes than Americans under both primes, the modulation of this main effect of culture by perceptual primes indicates the high malleability of these attentional effects.

Memory also appears to be susceptible to cultural influences on attention. Masuda and Nisbett (2001) showed Japanese and American participants animated scenes of fish swimming in a stream. Participants described the contents of each vignette. Japanese participants tended to make more statements that described contextual features of the backgrounds and relationships between objects in the scenes as compared to the

American participants. In a subsequent recognition test, participants were shown previously seen fish as well as novel fish. Each fish was either in its original setting or in a novel setting. Participants were asked to judge whether each fish was previously seen or not. A similar recognition memory task was also administered using pictures depicting animals in scenes. The results from the two memory tasks were highly similar. Japanese participants were more accurate at remembering previously seen fish or animals when they remained in their original context. In contrast, manipulating context had little effect on Americans' ability to remember a previously seen object.

The attentional influence of cultural context on perception has been observed in the direction of eye movements when attending to a visual scene that consisted of a single focal object or figure imposed on a realistic background (Chua et al., 2005). European Americans and Chinese participants viewed such scenes while their eye movements were recorded, and later completed a recognition memory task. During initial presentation of each scene, Chinese participants made more fixations on the background than did Americans, and took longer before the onset of the first fixation on the focal objects. Americans, in contrast, fixated on the focal objects for a longer time than did Chinese. Notably, the cultural differences that were observed all occurred relatively late in perceptual processing (>420 ms after scene onset), indicating that late-stage attentional processes were likely responsible for cultural differences in the visual search patterns. These results also suggested that cultural influences on visual attention extend to later memory, as a recognition test for the objects in each scene was administered for the same subjects, using procedures similar to those in the study by Masuda and Nisbett (2001). As demonstrated in Masuda and Nisbett, Chinese participants were more likely to correctly recognize an object when it remained in its original background context than when it was presented on a different background, whereas Americans' memories were unaffected by the background manipulation. It is important to note that these effects of culture on the guidance of eye movements have not been replicated in at least two subsequent studies (Evans et al., 2009; Raynera et al., 2007). Although the study by Chua et al. (2005) provides a clear demonstration of the concept, it is evident that further study is needed to clarify the effects of culture on visual saccade patterns.

In addition to cultural influences of attention on perception and memory, cultural differences in attention appear to affect judgments and reasoning about semantic relationships. One early study demonstrated that cultural differences in such attentional effects likely begin at an early age (Chiu, 1972). Chinese and American children were shown pictures of three objects such as a man, woman, and baby. American children tended to group objects based on analytic features or shared categories, for example, grouping the man and woman because they belong to the shared category of adults. Chinese children, in contrast, tended to group objects based on relational and contextual information, for example, grouping the woman and the baby because of their shared relationship (e.g., ‘‘the mother takes care of the baby’’).

Ji et al. (2004) later showed that these culturally specific tendencies extended to bilingual college students, testing participants in either English or Chinese to show that the results were not attributable to testing language. Their results confirmed the findings from Chiu (1972) that European Americans tend toward taxonomic organizations, whereas Chinese tend to rely on relational organizations. Furthermore, Chinese participants tended to group items in a more relational and less categorical way regardless of testing language. One interesting nuance was the finding that although Chinese participants had a consistent preference for relational organizations, this tendency was more pronounced in Chinese participants from the Mainland and Taiwan when they were tested in Chinese as compared to English, an indication that cultural modes of thought may be influenced or activated by certain priming manipulations.

Such cultural influences on attentional effects in patterns of eye movements, perception, memory, and reasoning that guide individuals to focus primarily on contextual relations or on focal objects has implications that extend to art and esthetic preference in East Asian as compared to Western cultures. Masuda et al. (2008) analyzed traditional artistic styles, contemporary art, and portrait photography in these two cultures. The authors examined traditional artistic styles using archival data in representative museums and also examined how contemporary East Asian and Westerners draw landscape pictures and take portrait photographs. Their analyses found that East Asian landscape paintings consisted of more contextual field information than did Western paintings. In portraits, East Asians painters and photographers deemphasized the face as measured by overall area than did Western painters and photographers. East Asian paintings were also more likely than Western paintings to depict field information. These results demonstrate that East Asian art has predominantly context-inclusive styles whereas Western art has predominantly object-focused styles, and imply that cultural predilections in visual attention may influence (and be influenced by) cultural expressions in esthetic sensibilities as measured in actual art samples.

In general, findings from behavioral studies indicate that cultural influences on attentional preferences that orient an individual toward contextual relations or toward focal objects and their attributes arise at an early age (Chiu, 1972; Duffy et al., 2009; Vasilyeva et al., 2007), are malleable, and can have extensive influences on visual perception, memory representation, reasoning about semantic relationships, and esthetic preferences. In addition, the likelihood of observing cultural influences of attention appears to be greater in more complex, higher-level cognitive operations such as reasoning, causal attribution, and esthetics, but culture may influence even lower-level processes through the operation of attention. These cultural influences differ across individuals within a culture, and can be modulated by even moderate experience within other cultural contexts.

Neuroscience of attention and object processing

As the above review indicates, behavioral studies have often observed differences in attention-related processing across cultural contexts, with East Asians preferentially attending to contextual information and Westerners preferentially attending to focal objects and their attributes. Under the assumption that cultural influences on mental states and processes will be reflected in regional differences in neural activation, and that a fuller understanding of the types of processes being affected by culture can be elucidated by investigating these neural correlates, several researchers have begun to examine the influences of cultural contexts with neuroimaging techniques (see review by Han and Northoff, 2008). Although the most compelling explanation for culture differences in perception, memory, and judgment observed at the behavioral level remains an account focused around cultural influences on attention, it is difficult to test directly the processes on which culture might operate with purely behavioral methods.

Multiple studies have examined the American tendency to focus on objects and their attributes and the East Asian tendency to focus on contextual relationships using neuroimaging technology. These neuroimaging studies have used a variety of paradigms, usually adapted from the behavioral literature, and do not always appear to be congruent with one another. However, these studies have begun to provide an emerging picture of how neural mechanisms may be selectively evoked by individuals from different cultural contexts. We note that a number of other neuroimaging studies on cultural influences have employed tasks or produced findings that can reasonably be interpreted as reflecting attentional interactions with other areas of cognition (Adams et al., 2009; Chiao et al., 2008, 2009; Freeman et al., in press; Zhu et al., 2007). In the current review, we focus solely on the few neuroimaging studies that have most directly investigated cultural influences on attention and its possible relationship to perceptual processing using relatively abstract task situations.

One of the key questions regarding cultural differences in cognition regards the exact mental processes by which culture might influence perception and memory. Gutchess et al. (2006) adapted the paradigm of showing scenes that consist of a single focal object and a rich contextual background (e.g., Chua et al. 2005; Masuda and Nisbett, 2001) for use with event-related functional magnetic resonance imaging (fMRI), scanning East Asian and American participants. Participants were shown pictures of a target object by itself, a background scene without a target object, and pictures of a background scene combined with a target object. Participants completed a surprise recognition task after the scan. Americans and East Asians displayed activation in similar brain regions during processing of background images. However, Americans tended to display greater activation in some regions during processing of objects. These included bilateral middle temporal gyrus, left superior parietal and angular gyrus, and right superior temporal/supramarginal gyrus. These results confirm behavioral evidence that Americans have a preference for processing analytically, in particular for target images versus processing holistically such as background images. Although the authors concluded that these cultural differences in neural activation reflect an early stage of encoding, the regions found to differ across cultures involved several attention-associated areas (such as superior parietal cortex and angular gyrus) and perceptual regions previously shown to be affected by top-down attentional modulation (Gazzaley et al., 2007; Yi and Chun, 2005). These cultural differences did not appear to influence later memory, as no significant difference in recognition memory was observed across cultures. This early study exhibits two traits that characterize many of the neuroimaging results regarding cultural influences on perception and attention. First, there were many similarities in perceptual processing across cultures. Second, the cultural differences that were observed are generally limited to higher perceptual regions that might be influenced by attention and to regions known to be associated with attentional processing.

Goh et al. (2007) used similar stimuli in a paradigm that exploits functional adaptation (Grill-Spector and Malach, 2001), or the tendency of the blood oxygenation level–dependent (BOLD) response to decrease in the presence of repeated presentations (also observed during repetition suppression and priming; Horner and Henson, 2008). Specifically, Goh et al. examined whether cultural experience affected the adaptation to repeated presentations of central objects and background contextual features. This study also included a comparison between younger (mean age 21.5 years) and older (mean age 67.4 years) adults within American and East Asian samples. Participants were shown pictures of objects imposed on background scenes. Scenes were repeatedly shown in succession, with independent manipulations of whether the object or background was the same or novel across repetitions. Although there were age effects within each culture in the adaptation response to repetition, differences between the cultures were not observed in the younger group and limited differences were observed among the older group. In particular, older Americans showed greater adaptation to repeated objects in the right lateral occipital complex, an area previously shown to be involved in object processing (Chee et al., 2006), than did older East Asians. In contrast, adaptation to backgrounds did not differ across cultures in either age group. Because Americans are assumed to pay more attention to objects, these results indicate that the adaptation response may be sensitive to cultural influences of attention. However, because the adaptation response occurs early in visual processing, these cultural influences were interpreted to be primarily automatic and outside the realm of volitional attention (Goh et al., 2007). The authors interpreted the cultural difference among the older, but not younger, groups as indicating that increased experience within a cultural context likely exacerbates the influence of cultural predilections on cognitive processing and associated neural responses (see theoretical discussion in Park et al., 1999). Although these findings provide limited neuroimaging evidence for cultural differences in perceptual processing of objects (Chua et al., 2005; Masuda and Nisbett, 2001; Masuda et al., 2008), there are several limitations to the data. Significant cultural differences were observed only among older adults and not among younger adults, were significant only in one hemisphere, did not reach significance for the full culture × age interaction, and were significant only in region of interest analyses rather than at the whole-brain level. Perhaps of most importance, culture effects were observed only in adaptation to objects, but not backgrounds. These limitations indicate that cultural influences on such early-stage perceptual and attentional responses may be relatively small.

Lewis et al. (2008) examined cultural influences on attention using the oddball paradigm with event-related potentials (ERP). European American and East Asian American participants were presented with infrequent target (the number 6) and frequent, or standard, nontarget (the number 8) stimuli. Rarely, infrequent nontarget stimuli (consonant or number triads, such as TCQ or 305) were presented. Target stimuli, as compared to standard stimuli, reliably elicit a response 300–400 ms after stimulus onset that is referred to as the target P3. Infrequent nontargets reliably elicit a P3 response with a different scalp distribution, referred to as the novelty P3. European Americans tended to display greater target P3 amplitudes than East Asian Americans, indicating that they primarily attended to the target events, giving them special status as compared to standard and infrequent nontargets. In comparison, East Asian Americans displayed greater novelty P3 amplitudes than did European Americans, indicating that they assigned special status to infrequent nontargets as compared to standard nontargets. In addition, these differences were correlated with an individual's self-construal, as measured by the Triandis (1995) Individualism and Collectivism Attitude Scale. Specifically, the more an individual (of either culture) expressed an interdependent self-construal, the more his or her novelty P3 response mediated the relationship of culture and the novelty P3. No significant correlations between target P3 and self-construal were observed. Based on the idea that the target stimuli are the focal objects (as only these identified targets required a response) and standard nontargets provide the general context in this abstract task, these findings are consistent with the research reviewed here that European Americans attend primarily to the focal object while East Asians are more sensitive to contextual features and disruptions (as represented in this case by the triad form of the infrequent nontargets). Furthermore, the relationship between interdependent self-construal and the novelty P3 response indicates that individual differences within a cultural context are important to understanding these effects and that high-level views of the self may have unexpected consequences on relatively abstract tasks, presumably via the direction of attention toward certain features of the environment. An additional advantage of the ERP method is its temporal sensitivity, allowing the cultural influences to be localized to 300–400 ms after stimulus onset, which is relatively late in visual processing (as neural signals faster than 100 ms are associated with object recognition; Liu et al., 2009). This indicates that cultural influences likely occur primarily during late-stage attentional processing.

Another study (Hedden et al., 2008) that specifically examined cultural influences on the neural correlates of attentional processing adapted the behavioral paradigm developed by Kitayama et al. (2003). East Asian and European American participants were shown a series of stimuli consisting of a line within a surrounding square while undergoing fMRI. For each stimulus, participants judged whether the length of the vertical line inside the box matched the length of the line in the previous stimulus. Stimuli were shown in blocks, with an instruction (either absolute or relative) preceding each block. Using the absolute instruction, participants were to judge whether the current line matched the previous line in absolute length, regardless of the size of the square. Based on previous findings (Kitayama et al., 2003; and see also Duffy et al., 2009; Vasilyeva et al., 2007; Zhou et al., 2008), absolute judgments are assumed to require processing of the line independent of the surrounding context, a task that Americans are presumed to prefer and to process more fluidly than do East Asians. In contrast, when using the relative instruction, participants judged whether the current line matched the previous line based on its ratio to the square in each stimulus. Relative judgments are assumed to require processing of the line in a manner that is interdependent with its surrounding context, which East Asians are presumed to prefer and process more fluidly than Americans. In contrast to some behavioral studies (Duffy et al. 2009; Kitayama et al., 2003), no performance differences were observed across the cultures, likely because the task had been simplified for use in the scanner (and perhaps due to the much smaller sample size, and thus lower statistical power, than in the Kitayama et al., study). Nonetheless, a striking interaction (see Fig. 1b) was observed in the BOLD response in a variety of attention-related regions, with each cultural group displaying greater activation during the instruction condition in which their cultural preference was not engaged (i.e., the relative instructions for Americans and the absolute instructions for the East Asians). These regional increases in activation suggest that each culture processed the nonculturally preferred task less fluidly than did members of the opposite cultural group.

Furthermore, Hedden et al. (2008) found that activation in these attention-related brain regions was correlated with self-report scores on questionnaires that measured individual differences in culture-typical identity. Americans completed a questionnaire that measured independence/ interdependence (e.g., “I am not to blame if one

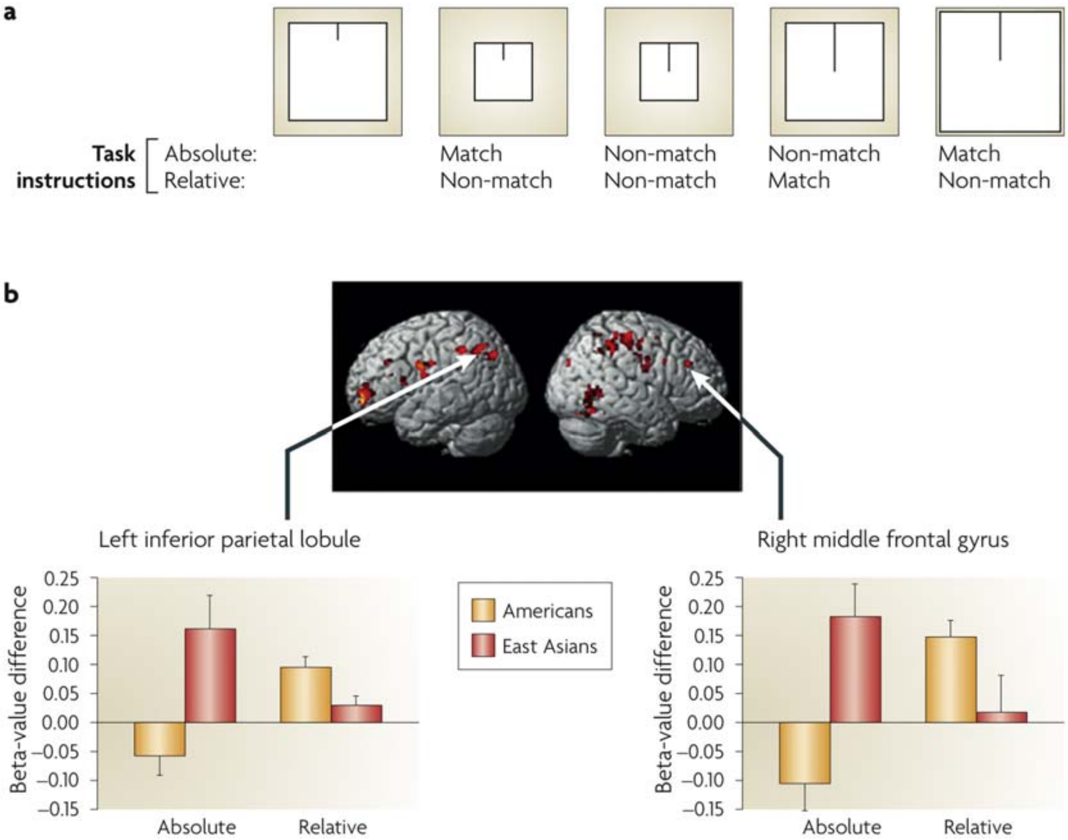

Fig. 1. (a) Participants judged whether the length of a vertical line inside a box matched the length of a previously shown line regardless of the size of the box (a context-independent (absolute) judgment task), or whether the box–line combination of each stimulus matched the proportional scaling of the preceding combination (a context-dependent (relative) judgment task). (b) Frontoparietal activation associated with judgment tasks in Americans and East Asians. Activity was greater in East Asians (red bars) than in Americans (yellow bars) in the context-independent (absolute) judgment. The opposite was observed in the context-dependent (relative) judgment task. Adapted with permission from Hedden et al. (2008) Blackwell and by permission from Publishing from Macmillan Publishers, Ltd: Nature Reviews Neuroscience, Han and Northoff (2008). Please see online version of this article for full color figure.

of my family members fails;" Triandis et al., 1988). Of note, this questionnaire was incorporated during development of the IND/COL scale (Triandis, 1995) used in the study by Lewis et al. (2008). East Asians, all of whom had been living in the United States for less than 7 years, completed a questionnaire that measured their degree of acculturation (e.g., "How well do you fit in with other Asians of your same ethnicity;" Suinn et al., 1992). Within each culture, scores on these questionnaires were related to the regional BOLD response in the attention-related brain areas. That is, Americans with less activation during the absolute instructions and greater activation during the relative instruction were more likely to express a higher degree of independence. Similarly, East Asians with less activation during the absolute instructions and greater activation during the relative instruction were more likely to express a higher degree of acculturation to American culture. In general, the degree to which individuals within both cultural groups expressed attitudes and beliefs that correspond to independent, Americanized ideas was related to the degree to which their patterns of brain activation reflected an ease of processing during the absolute (American-preferred) instructions and more difficulty of processing during the relative (East Asian-preferred) instructions. Notably, the regions involved in the computation of these correlations were not identified on the basis of possessing a correlation, so that these results are not susceptible to the nonindependence error described by Vul et al. (2009).

Finally, support for the role of individual differences was found in a subsequent analysis of the Hedden et al. (2008) study by Aron et al. (under review). Aron et al. found that for individuals with a temperament trait characterized by focus on the details of stimuli (high sensory processing sensitivity, Aron and Aron, 1997) and unrelated to the measures of cultural identification, there was little or no cultural difference in response to the absolute versus relative tasks. But those without this temperament trait showed especially strong cultural differences (i.e., there was a large, significant three-way interaction of culture × task × temperament).

More generally, the study by Hedden et al. (2008) highlights three important points regarding cultural influences on cognition. First, cultural influences appear to be the most prominent in brain regions associated with relatively late-stage attentional processing, rather than early visual processing. This point is also evident from the timing of responses in the Lewis et al. (2008) study, in several of the observed regions in the Gutchess et al. (2006) study, and in the small effects in perceptual regions in the Goh et al. (2007) study. However, this does not imply that such cultural influences on attention are volitional in nature; indeed, the attentional preferences attributable to cultural influences are likely unknown to the individuals who exhibit them. Second, cultural influences appear to be primarily found in the extent to which these attention-related regions display differential activation across cultures. That is, the same task-relevant regions were generally observed across cultural groups, but the level of activation in these regions under certain task situations was modulated by culture, a point reinforced by the cultural similarities found in almost all functional imaging studies of culture to date. And third, cultural influences on attention appear to be related to individual differences. In particular, individual differences in independent and interdependent self-construals within cultures mirror the between-culture differences, a point also supported by the Lewis et al. (2008) findings. Other individual differences, such as a temperamental tendency to focus on details of stimuli, may also moderate cultural effects on attention, functioning to undermine or accentuate them.

Conclusion

Cultural neuroscience is a still-developing field that exhibits promise for confirming and extending behavioral research on cultural differences in attention and related processes. Despite the relatively few studies that have been conducted to date, there is already substantial evidence that the neural mechanisms underlying attention are shaped by one's cultural identity and upbringing.

Notably, findings from neuroimaging studies support hypotheses derived from behavioral experiments that regard the influence of cultural effects on attention and the mediation of these effects by interdependent and independent self-construal.

Neuroimaging data provide the opportunity to understand more precisely the mechanisms that underlie these cultural influences, which are sometimes difficult to interpret from purely behavioral metrics. The localization of cultural effects to particular brain regions involved in a task can point to the likely processes involved in these regions. Similarly, timing information (especially from ERP data) can provide additional information regarding the stage of information processing during which cultural influences are likely to occur. However, during the inferential procedure, one must be careful to avoid the problem of "reverse inference," in which mental processes are attributed to individuals from a given culture on the basis of brain regions or ERP components that are insufficiently associated with a particular cognitive mechanism. Nonetheless, these data provide an important source of additional information that may allow the detection and interpretation of cultural influences, in some cases in the absence of performance differences between cultures (e.g., Hedden et al., 2008).

This review has focused almost exclusively on two specific cultural contexts, East Asian and Western cultures, that have been extensively studied and appear to systematically differ in the self-construals that they encourage in their members (Hofstede, 1980). Western cultures, such as found in America, tend to emphasize focal objects, categorical groupings, and analytic reasoning styles that are associated with an independent self-construal. In contrast, East Asian cultures, such as those found in Japan, China, Taiwan, and Korea, tend to emphasize contextual or background features, relational groupings, and holistic reasoning styles that are associated with an interdependent self-construal (Markus and Kitayama, 1991; Nisbett et al., 2001; Triandis, 1995). These values presumably become ingrained in how individuals from these cultures view themselves and the world. Almost inevitably, our cognitive processes will be informed, shaped, and modulated by these cultural values. One likely important nexus for such cultural influences is cognitive processes related to attention. Attention is a likely target for environmental influences in general, of which culture can be considered a specific example. Attention orients our perception and interpretation to particular features in a complex field of incoming information, and colors how we search for and respond to salient attributes of the environment.

Almost no cognitive psychologist or neuroscientist would deny that environmental influences have substantial impact on the development and operation of attentional processes. To the extent that cultural influences are one form of environmental influence, it is likely that attention will be impacted to some degree by an individual's cultural upbringing. There are obviously many dimensions along which cultural contexts (and national and linguistic contexts, which are highly overlapping with culture) vary. Although differences in self-construal are a current major candidate for the central influence of cultural context on cognition, further research is clearly needed to identify other candidate dimensions and the relative importance of these various dimensions in explaining cultural variation in attention and cognition.

Investigations of culture using both behavioral and neuroimaging techniques consistently point out that attention and other cognitive processes are reliably invoked in much the same way across cultures, but are modulated in specific ways by one's cultural upbringing. It is therefore important to keep in mind the similarities in information processing across all humans in interpreting the ways in which we vary across cultural contexts. Against this backdrop of similarities, cultural influences are more likely to be analogous to "tuning" processes during neural development, in which small adjustments are made to synaptic plasticity across long periods of experience, rather than to "pruning" processes, in which unreinforced synaptic connections are lost. In sum, cultural context appears to be a potentially important variable in understanding the range of human cognition, and may provide a window into the mechanisms by which individual differences in cognitive processing arise. Attention is likely to be a central process through which such cultural variation may have its impact on other areas of cognition, and such cultural influences appear to be more likely to occur in later stages of attentional processing than in earlier stages of perceptual processing.

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SECTION III

Cultural Neuroscience of Cognition

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CHAPTER 7

Culture sculpts the perceptual brain

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Abstract: Cultural differences in the way Westerners and East Asians perceive and attend to visual objects and contexts have now been shown across many behavioral studies. Westerners display more attention to objects and their features, in line with an analytic processing style, whereas East Asians attend more to contextual relationship, reflecting holistic processing. In this article, we review these behavioral differences and relate them to neuroimaging studies that show the impact of cultural differences even on ventral visual processing of objects and contexts. We additionally consider the evidence showing how extended experience within a culture via aging affects ventral visual function. We conclude that the brain findings are in agreement with the analytic/holistic dichotomy of Western and East Asian visual processing styles. Westerners engage greater object-processing activity while East Asians engage more context-processing activity in the ventral visual areas of the brain. Although such cultural imaging studies are still few, they provide important early evidence supporting the importance of cultural experiences in sculpting visual processing at the neural level.

Keywords: culture; ventral-visual cortex; neuroimaging; objects; contexts

Introduction

The influence of culturally different experiences is evident in the way we perceive and process the visual world. These cultural differences may be a result of prolonged exposure to different cultural values, viewpoints, behavioral practices, and possibly even visual environments, that subsequently biases the processing of visual information (Chiao et al., 2008; Miyamoto et al., 2006; Nisbett et al., 2001; Nisbett, 2003; Nisbett and Miyamoto, 2005). In particular, Westerners, who are embedded in an independent culture (Hong et al., 2001; Markus and Kitayama, 1991; Schwartz, 1990; Triandis, 1995), acquire more analytic processing styles that have been related to greater attention to objects and their features such as color, shape, and size (Nisbett et al., 2001; Nisbett and Miyamoto, 2005). Such analytic visual processing emphasizes the constancy of object attributes regardless of the contexts in which the object occurs. In contrast, East Asian culture is characterized by a focus on the interdependence of the individual with others and with the surrounding contexts, which biases the individual toward more holistic processing involving greater attention to contexts and the relationships between different items or objects. Thus, in holistic processing, representations of objects are more intimately linked to, and dependent on, the context. Recent neuroimaging studies are beginning to uncover subtle but consistent

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neural correlates of such cultural differences in visual processing between Westerners and East Asians (Han and Northoff, 2008). These imaging findings are largely in agreement with a greater bias toward object processing in Westerners, and context processing in East Asians, as evinced by their respective functional brain responses in the ventral visual cortex. In this article, we jointly consider the behavioral and neuroimaging evidence in support of these cultural differences in visual processing in Westerners and East Asians. We also discuss the role of extended cultural experience that occurs with aging, considering the hypothesis that cultural biases in visual cognition become more pronounced with age as a result of accrued experiences over time (Park et al., 1999; Park and Gutchess, 2006).

We begin with the behavioral evidence that demonstrates cultural influences on perceptual and attentional processing in terms of sensitivity to visual objects and contextual information. Next, we highlight some important methodological and conceptual issues related to the interpretation of current neuroimaging studies on cultural differences. We then present neuroimaging evidence across multiple studies that indicate that cultural experiences affect functional differences in the ventral visual cortex, a critical brain region for visual perceptual and attentional processing. Finally, we conclude with a consideration of how cultural experiences and aging jointly modulate ventral visual activity, addressing the interrelationship between sustained life experiences that occur within a culture in the context of neurobiological declines in brain structure and function associated with aging.

Cultural differences in perception and attention to objects and contexts

A number of studies have yielded behavioral evidence for cultural differences in perception and attention of visual materials. We should note that when we refer to “visual perception” we are defining this construct as the individual’s phenomenological experience and interpretation of the visual sensory information (Garrett, 2009). Perception is closely linked to, and may be partially dependent on, attention. Attention refers to the selection of specific information within the visual representation, usually by enhancing processing of the selected items or by inhibition of nonselected items, or both (James, 1890).

The influence of culture on perception is revealed when examining how Westerners and East Asians differentially perceive the same visual information, particularly with respect to variations in context. Kitayama et al. (2003) used the Frame-Line Test to evaluate how individuals from Western and Eastern cultures are affected by visual contextual information. In the Frame-Line Test, participants view a line presented within a surrounding square frame of a fixed sized during the study phase. During the test phase, participants are presented with an empty square frame that is of a different size. Participants are then asked to draw a line in the square using either relative judgment, so that the ratio between the line length and the square size is preserved as in the study phase, or using absolute judgment, so that the square size is ignored and the line length is maintained as in the study phase. The results of this study are shown in Fig. 1. Figure 1 shows that Westerners were better at absolute judgment, and were less affected than East Asians by the change in contextual square frame size, whereas East Asians were better at the contextually based relative judgment.

In another study by Masuda and Nisbett (2001), participants viewed short video clips containing focal objects that interacted with each other within a contextual environment. During a subsequent recall test, East Asians were more likely to recall information regarding the background scenes whereas Westerners recalled more detail about the focal objects. Ji et al. (2000) also found similar cultural biases such that East Asians were more sensitive to information regarding the co-occurrence of pairs of objects and were more affected by the contextual frame when determining rod orientations compared to Westerners. In an interesting use of photography to study aesthetics in visual perception, Masuda et al. (2008) found that East Asians were more likely to photograph portraits that contained more

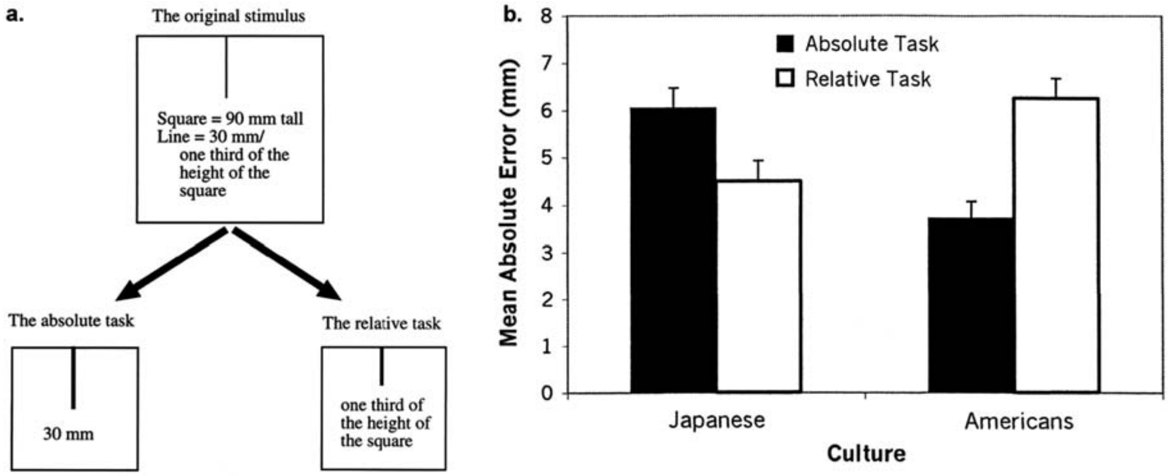

Fig. 1. (a) In the Frame-Line Test, participants view a line presented within a surrounding square frame of a fixed sized during the study phase. During the test phase, participants are tasked to either draw a line in a square of different size using relative or absolute judgments. (b) Westerners (Americans) were less affected by the change in square frame size at test and were better at absolute judgments, making fewer errors than Easterners (Japanese), whereas Easterners were better at relative judgments. Figure adapted with permission from Kitayama et al. (2003).

contextual background while Westerners tended to take portraits with the person's face occupying a larger proportion of the picture. This growing body of behavioral findings consistently shows that Westerners perceive visual information more in terms of features and constant attributes that are less bound to the context whereas East Asians perceive relationships among features and may engage more contextually bound representations.

Cultural differences in attention to specific elements in visual stimuli have also been demonstrated and may fundamentally drive perceptual experiences. A clear case for this is seen in cultural studies that have used the change-blindness paradigm in which some part of a rapidly flashing picture is repeatedly modified but due to an inability to attend to the entire picture, some time is required before the change is detected (Simons and Levin, 1997). Masuda and Nisbett (2006) used the change-blindness paradigm and selectively modified either a central object in the picture, or a background scene element. They found that although participants from both groups were just as fast at detecting object changes, East Asians were faster than Westerners at detecting visual changes that occurred in background scenes. In subsequent experiments, Masuda and Nisbett (2006) also found that Westerners were also more likely than East Asians to detect changes occurring in the focal objects. Similarly, in a very recent study, Boduroglu et al. (2009) showed that Westerners were better at detecting color changes when they occurred within the central portions of the screen whereas East Asians were better when color changes occurred in the background or peripheral location. These findings suggest that attentional processes in East Asians were biased toward detecting information in the visual background scenes, at least more so than in Westerners.

Direct evidence for differential attention to specific visual elements has also been demonstrated in culturally different eye movements to visual stimuli. When viewing scenes with embedded central objects, Westerners' fixation durations were longer and thus more focal, while East Asians had shorter fixation durations and fixated more often on the background (Chua et al., 2005). We also examined attention to objects and background in complex scenes utilizing an eye-movement paradigm. We selectively changed central objects or background information in a scene. Such changes of selected elements would generate a strong attentional capture for

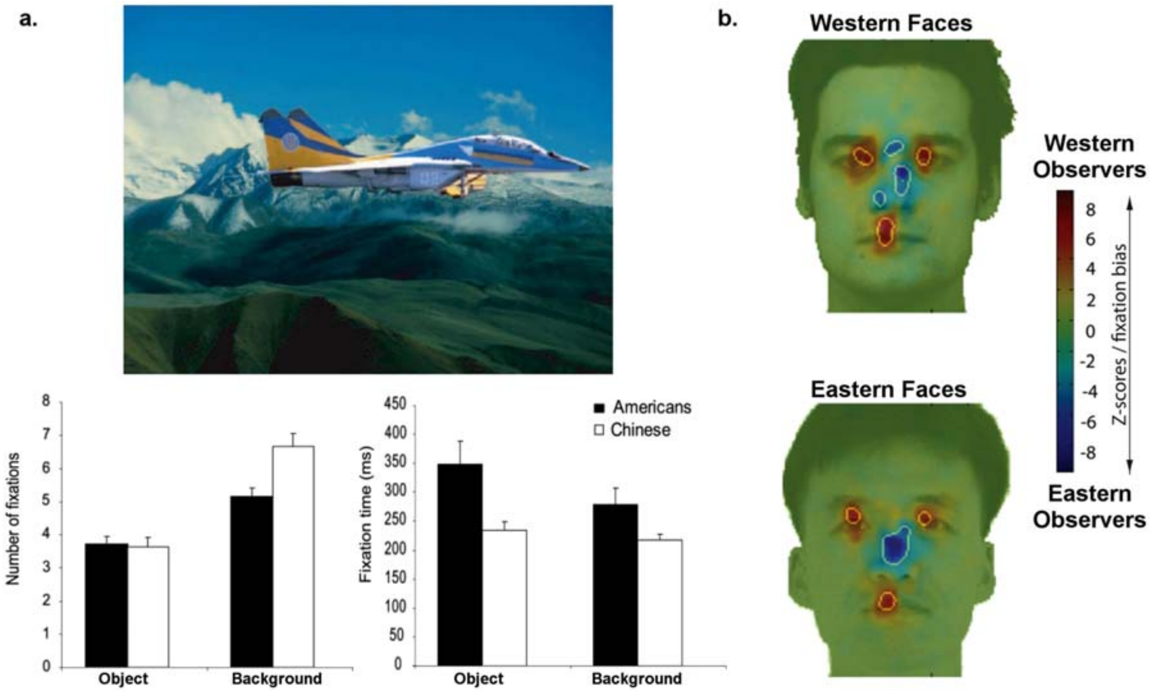

Fig. 2. (a) When viewing scenes with embedded central objects, Westerners' fixation durations were longer while Easterners had shorter fixation durations and fixated more often at the background (adapted with permission from Chua et al., 2005). (b) When viewing stimuli consisting of Western and Eastern faces, Westerners consistently made more fixations on the eyes and mouths whereas Easterners focused centrally on the nose regardless of the ethnic background of the face (adapted with permission from Blais et al., 2008).

eye movements toward the changed items.[1] Nevertheless, cultural differences were still observed such that Westerners' eye movements were more affected by object change than East Asians (Goh et al., in preparation). Further, East Asians' eye movements alternated more between objects and backgrounds consistent with a bias to process contextual relationship between objects and their contextual scenes. An interesting speculation from these eye-movement findings for scene viewing is that focal fixations on scenes in Westerners may reflect the processing of detailed featural information about individual objects within a scene with fewer saccades across scenes and longer fixation durations to maximize high-resolution foveal input. In contrast, scene viewing in East Asians involves rapid changes in representations as the eyes fixate on a visual locus and quickly move on to the next. Contextual scene representation is thus potentially more dynamic in East Asians.

Cultural differences in eye movements also extend to face viewing. Blais et al. (2008) showed that when participants viewed face stimuli, eye movements in Westerners consistently focused on the eyes and mouths whereas East Asians focused centrally on the nose (Fig. 2b). They speculated that this is because East Asians generally consider it socially inappropriate to look directly into a person's eyes. The Westerner's pattern of eye movements for faces is consistent with the processing of detailed visual information such as eye shape and color, along with configurations of facial components that reflect the importance of

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[1] The visual changes in this study occurred in the order of seconds. Thus, there is an attentional direction to visual novelty unlike the change-blindness paradigm in which changes are rapidly occurring at the millisecond level resulting in a failure of detection.

representing distinctiveness of face identities, important in an independent culture that values individualism (Chiao et al., 2009a; Hong et al., 2001; Nisbett et al., 2001; Nisbett, 2003; Schwartz, 1990).

The eye-movement data provides a great deal of insight into where attention is directed and provides evidence as to how attentional focus acts as a mechanism to accent particular components of the visual information while other components are inhibited. Culture differences in attentional focus affect how information is perceived, encoded, stored in memory, and subsequently retrieved later on. It is also worth noting that cultural differences are not always found in eye-movement studies, even in situations where they might be expected. For example, Rayner et al. (2007) did not find any differences between Westerners' and East Asians' eye movements when participants viewed scenes consisting of several identifiable objects. When the scene contained only one central object, however, East Asians fixated more often on the background, replicating Chua et al.'s (2005) finding. Also, Rayner et al. (2009) presented Westerners and East Asians with pictures containing specific regions with incongruent information (such as a man with a disproportionately longer right arm). In that study, the authors found no differences between Westerners and East Asians in eye movements toward the incongruent regions. These findings demonstrate that interesting or important content of visual scenes may sometimes take precedence and eliminate the effects of culture on visual processing. Despite these findings, it is important to recognize that when cultural differences are observed in eye movements or perceptual tasks, the findings are generally consistent with object-focused processing in Westerners and context-focused processing in East Asians. This cultural dichotomy for object versus contextual processing presents a convenient lead into the evaluation of how these visual processing differences are manifested in the brain. We therefore consider next, the findings regarding the ventral visual cortex — its role in processing objects and the contexts in which they occur and the evidence showing cultural differences in the neural processes involved.

Cultural differences in ventral visual brain function

Methodological considerations

Before discussing the neuroimaging findings in detail, we first consider some nuanced methodological issues that are related to data acquisition, analysis, and interpretation, and are relevant to studies of neural differences between cultures. The study of culture differences is challenging for many reasons, probably the most notable relating to obtaining participant samples that are saturated with culture-specific experiences, yet equated on other factors such as cohort experiences, education, health, and other demographics (Manly, 2008a, b; Park, 2008; Park et al., 1999; Schaie, 2008; Whitfield and Morgan, 2008). This sampling issue is particularly difficult for neuroimaging data acquisition, given the cost of conducting imaging studies and the relatively low reliability of functional imaging signal. A variety of methodologies across different neuroimaging studies of cultural differences have been utilized to deal with sampling issues.

One approach to sampling is to obtain representative samples from each culture by recruiting participants within their home countries and determining that both groups show similar distributions on some variable, such as speed of processing or a subtest of an intelligence test (Park et al., 1999). This ensures that individuals occupy the same relative position on a variable within each culture. The problem with sampling participants from different locations for neuroimaging studies is that the neuroimaging hardware is confounded with the culture being tested (Park and Gutchess, 2002) and thus requires very careful matching of the signal properties from the two different imaging machines. Figure 3 shows data from a study conducted in our lab at two sites (Singapore and the United States). It was expressly designed to address the validity of conducting cross-cultural neuroimaging studies at two different sites. The same American and Singaporean subjects were imaged on a visual and motor task in identical 3 Tesla MRI machines at both sites using the same pulse sequences and the

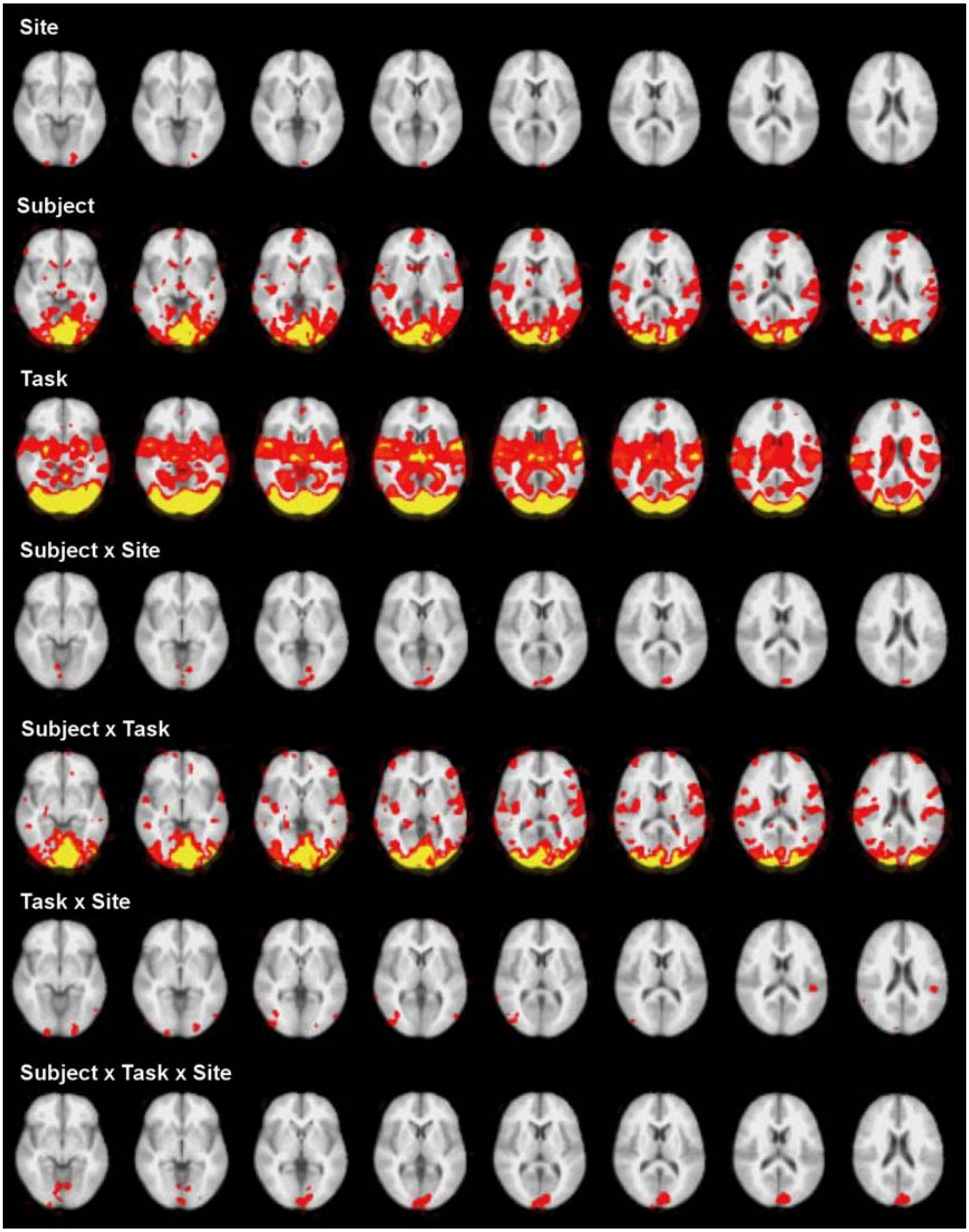

Fig. 3. Data from a study that compared identical magnet systems from two sites: Singapore and the United States (adapted with permission from Sutton et al., 2008). The same participants performed the same tasks at both magnet sites. Voxels for which the labeled effects were significant $p < .001$ are colored with increasing red intensities. The main effects and interactions of subject and task were by far the most prominent. The main effect of magnet site and its interactions with the effects of subject and task were negligible. Please see online version of this article for full color figure.

signal properties were compared (Sutton et al., 2008). While there were some small differences in the overall functional signals between the two magnets, these effects were negligible compared to the reliability of subjects' task-related functional activation across sites. Critically, the interactions of magnet site with the subjects or task were minimal, providing evidence for direct comparability of signal from two different magnets in two countries. Data from this study and others show that comparisons of cultural differences where magnet is confounded with culture are feasible, but great care needs to be taken to assess signal properties. Other studies comparing cross-site magnets have reached similar conclusions (Casey et al., 1998; Cohen and DuBois, 1999; Ojemann et al., 1998; Specht et al., 2003).

In many cases, however, obtaining imaging data from two geographically different sites is not feasible. The majority of cultural imaging studies sample East Asian participants who have recently entered a Western country, typically as students, and they compare their performance and brain data to Western students at the same institution, using only one MRI machine for the study. The assumption is that the East Asian participants have not been exposed to the Western culture long enough for the Western culture to influence cognitive processing in significant ways. One problem with this assumption is that it may not be completely valid as evidence suggests that even short exposures to different cultural modes of thought can bias subsequent processes (Chiao et al., 2009b; Miyamoto et al., 2006). Another problem with such samples is that such individuals are often a select group of students or individuals who have gained opportunities to study or work overseas based on their outstanding performance in the home countries. This may have the effect of limiting within-group variance if the high-performing individuals are a relatively homogenous select sample, while simultaneously accentuating between-group variance if the Western sample is not as highly selected for achievement as the East Asian sample. This could result in conclusions of cultural differences that in fact are associated with selection factors. Nevertheless, if cognitive differences are still observed in such samples when levels of education and abilities are tested and equated across groups, then it is more probable that the observed differences are associated at some level with true cultural differences. With regard to selecting appropriate tests to equate cognitive abilities, Hedden et al., (2002) provide data on simple and quick neuropsychological tests of speed of processing and working memory that appear to be culturally invariant and that rely more on visuospatial rather than numerical tasks, which typically show cultural biases (due to the lower syllabic density of numbers in Mandarin, for example). Overall, in cases where sampling participants in their home countries is not available, some form of neuropsychological testing is critical to ascertain comparability of basic cognitive abilities across groups.

Along with these methodological issues, the importance of using a strong framework with predictions should also be stressed (Park and Gutchess, 2002; Park et al., 1999). Fine-grained, a priori hypotheses are essential in directing neuroimaging research, given the complexity and multidimensionality of the data collected, particularly from functional imaging studies. In this article, we adopt the view of Nisbett and others and treat cultural biases in the visual processing of Westerners and East Asians as a result of their prolonged experiences within the different social and physical environments that promote analytic and holistic processing styles, respectively (Nisbett et al., 2001; Nisbett, 2003; Nisbett and Miyamoto, 2005). Over a period of several years, we have investigated these culture differences in the ventral visual cortex, based on the wealth of behavioral data regarding object and contextual processing cultural differences. We have tested the hypothesis that cultural experiences would sculpt ventral visual operations, utilizing functional imaging paradigms. We hypothesized that Western brains would show a bias to engage more regions specialized for object processing, and East Asian brains would engage more regions specialized for contextual or scene-processing regions or patterns of activity. This very specific, region-based hypothesis of ventral visual function is driven by the analytic/holistic cultural framework and is in contrast to conducting nonspecific culture contrasts that could conceivably reflect genetic or experience-based differences between the groups that are not a function of specific experiences and modes of thought. In addition, we have also examined the interaction of age and culture to address how the biological effects of aging and cultural experiences jointly affect function of the ventral visual cortex, as a great deal can be learned about the plasticity of the aging mind from these contrasts. To the extent that cultural biases are more prominently observed in older adults' neural activity compared to younger adults, it suggests that the sustained exposure to a culture contributes more to neural development with age. In contrast, if neurobiological aging is a more prominent factor in neural development than culture, older adults from the two cultures should become more similar in terms of ventral visual function (Park and Gutchess, 2002, 2006; Park et al., 1999).

Specialization in the ventral visual cortex

The ventral visual cortex is a large swathe of neural tissue that encompasses the occipital, fusiform, inferior temporal, parahippocampal, and lingual regions (Farah, 2000; Grill-Spector and Malach, 2004). This cortical region is involved in the identification and recognition and of visual stimuli (the ''what'' processing stream) in contrast to the location or spatial properties of stimuli (''where'' processing stream) that generally involves the more dorsal parietal regions (Mishkin et al., 1983). In particular, an important role of the ventral visual cortex is to parse incoming visual information into broad categorical domains such as faces, objects, and scenes for further processing in selective brain areas (Farah, 2000; Grill-Spector and Malach, 2004). One of the most consistently demonstrated functional patterns of brain activity in the ventral visual cortex is the selective engagement of separate regions for specific categories of visual stimuli (Epstein and Kanwisher, 1998; Goh et al., 2004; Grill-Spector, 2003; Grill-Spector et al., 1998, 2001, 2008; Kanwisher et al., 1997; Malach et al., 1995). Brain responses in the ventral visual areas when participants are viewing faces, objects, and houses are highly specialized and dissociated into clearly partitioned brain regions (shown in Fig. 4). When subjects passively view a series of faces, the face stimuli selectively engage the fusiform face area (FFA) as well as the occipital face area (OFA). In contrast to faces, the viewing of stimuli of outdoor scenes, including stimuli containing houses, tend to elicit higher activity in more medial regions of the ventral visual cortex including the parahippocampal place area (PPA), lingual gyri, and retrosplenial cortex. Stimuli containing pictures of objects typically engage more activity in the lateral occipital complex (LOC), which includes the inferior occipital regions extending into the inferior temporal and fusiform areas as well. This selective recruitment of highly specialized, stimulus-specific areas is robust across many individuals. It is also important to note that all visual stimuli engage a range of visual areas in the brain in a distributed manner, but the areas described here are maximally engaged when processing specific classes or categories of stimuli that share similar perceptual properties (Haxby et al., 2000, 2001; O'toole et al., 2005).

The reliability of ventral visual selectivity across individuals suggests that this pattern of neural function and engagement is relatively hard-wired in the neural circuitry, and one might expect little sculpting of these areas as a function of cultural experiences. Despite the breadth of evidence for selectivity, we considered that the perceptual and attentional behavioral data on culture suggested that it was certainly possible that cultural experiences might affect selectivity of neural regions used for processing various aspects of visual stimuli. There are a small number of studies that have addressed this possibility and the extant studies indeed suggest that culture does affect ventral visual selectivity and function.

Culture differences in ventral visual brain function

The first study to demonstrate culture differences in ventral visual activity was conducted by Gutchess et al. (2006). The investigators employed an incidental object-encoding task in an fMRI experiment. Participants viewed scenes

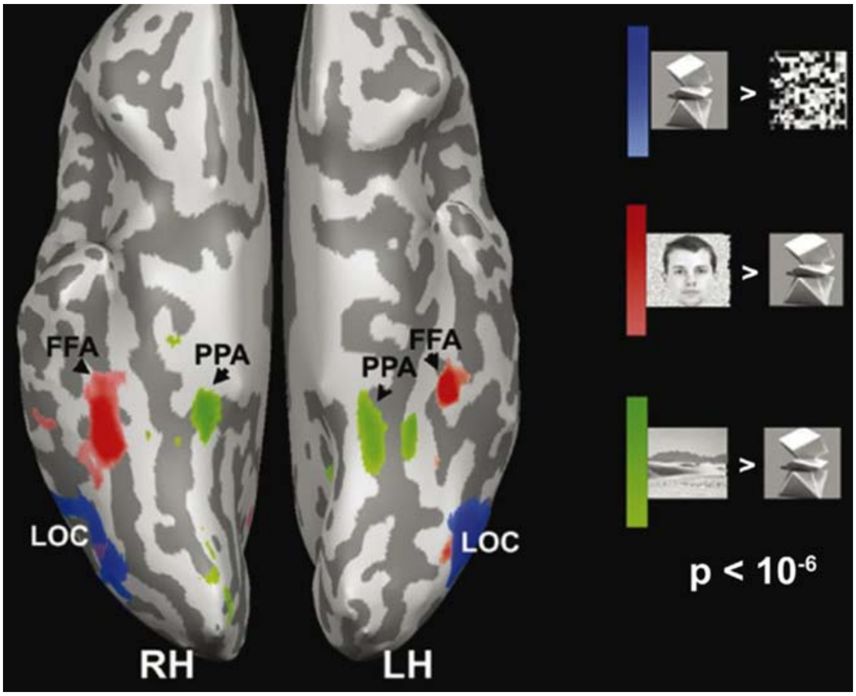

Fig. 4. Inferior view of the left and right hemispheres (LH, RH) of an inflated brain showing the ventral visual areas highly specialized for processing specific visual categories. The fusiform face area (FFA) is specialized for faces, lateral occipital complex (LOC) for objects, and parahippocampal place area (PPA) for scenes (adapted with permission from Grill-Spector et al., 2008).

where a central figure (e.g., an elephant, an automobile) was presented alone, or against the background of a meaningful scene (a jungle, a busy street). In a third condition, a meaningful scene was presented without the central figure (e.g., only a jungle or street without the elephant or automobile), and subjects made pleasantness judgments about the visual stimuli. The sample consisted of Western college students at a Midwestern university, and East Asian students from Hong Kong and other parts of China who had recently entered the United States and enrolled as students. The findings showed that Westerners engaged more object-related activity than East Asians in the lateral occipital region, a region known to be selective for object processing. The findings were consistent with greater object-focused processing in Westerners compared to East Asians, although no differences were found for scene-processing regions. It is possible that the pleasantness rating task biased participants to process more feature information about the objects and scenes, thus cultural differences for scenes and even objects may have been minimized due to task demands. Nevertheless, some evidence for cultural differences in object processing in the ventral visual stream was found.

In a later study, we examined ventral visual responses to face and house stimuli in Westerners and East Asians to evaluate how culture affects the highly reliable specialization of ventral visual activity for these visual categories (Epstein and Kanwisher, 1998; Goh et al., 2004; Grill-Spector et al., 1998, 2008; Kanwisher et al., 1997). In this recent and as yet unpublished study from our lab, we utilized a blocked-design fMRI experiment where subjects passively viewed face and house stimuli in the MRI scanner (see abstract: Goh et al., 2008). The sample consisted of East Asians from Singapore and Westerners from the United States, and involved two identical magnets with equivalent signal properties verified in a previous study (Sutton et al., 2008). Across both cultures, ventral visual specialization was reliably observed for faces and houses in the FFA and PPA, respectively among other brain regions. We also observed significant differences as a function of culture in selectivity that were consistent with the behavioral work and theorizing regarding East Asian/Westerner processing biases. Westerners showed more selective responses for faces compared to houses in the FFA that suggested a bias to represent faces with more distinctiveness and is consistent with an individualistic focus. This bias for more distinctive ventral visual face representations could reflect previously mentioned attentional factors in which Westerners eye movements tend to focus more on distinctive features on a face thus resulting in more selective FFA responses (Blais et al., 2008). This greater attentional focus could stem from greater face selectivity in FFA for Westerners may stem from more social factors related to a more independent culture in which Western individuals view themselves as distinct from others in terms of self-identity (Chiao et al., 2009a; Hong et al., 2001; Nisbett et al., 2001; Nisbett, 2003; Schwartz, 1990). Although we did not observe cultural differences in the PPA, East Asians showed more selectivity to houses compared to faces in the lingual areas, also a part of the ventral visual cortex that is more selective for houses than faces. Greater selectivity in house selective regions in East Asians is consistent with a bias toward processing more information about contextual differences and relationships. These findings reveal that while specialization of ventral visual areas for face and house stimuli is highly similar across cultures, there are subtle but culturally consistent effects with Westerners showing greater selectivity in face processing regions and East Asians showing greater selectivity in house processing regions.

In related work, we utilized an fMR-Adaptation paradigm (fMR-A) to study specialization of the ventral visual cortex for objects and places as a function of culture. The fMR-A paradigm provides a means of measuring differences in selectivity and specialization in the ventral visual cortex based on the phenomenon that brain response to repeated stimuli is typically reduced. This reduction in activation when a stimulus is repeated provides an index of the brain's ability to detect similarity between stimuli, and reflects the use of less neural resources to process information that is repeated. Goh et al. (2004) used this technique to isolate brain regions that were involved in processing objects from those involved in processing scenes. In that study, participants passively viewed quartets of pictures with each picture consisting of a central object embedded within a background scene (Fig. 5a). Within a quartet, the pictures were repeated such that either (a) the object and background scene were presented four times, or (b) the central object was changed across the quartet with the background scene held constant, or (c) the background scene was changed with the object held constant, or (d) both objects and backgrounds scenes were changed across the quartet of pictures. This selective repetition of pictorial components allowed Goh et al. (2004) to isolate brain regions that were sensitive to either object repetition (object-processing regions) or background scene repetition (scene-processing regions). The object regions were observed to be localized in the lateral occipital regions, whereas repeated scenes induced adaptation only in parahippocampal regions. This was a powerful replication of previous literature on ventral visual specialization because the fMR-A paradigm allows each subject to act as his or her own control as it is the relative decrease to repetition per subject that is of interest. Further, the design presented both objects and scenes in the same stimuli, while selectively repeating one of the components. Thus although both components are present in the stimuli, only the region that processed the repeated component would show adaptation, eliminating concerns about equating luminance, and visual composition across conditions.

The fMR-A paradigm was then used by our research group to study cultural differences in ventral visual engagement for objects and background scenes in Westerners and East Asians, while also examining the effect of age in young and older adults from both cultures. Using the same stimuli and adaptation paradigm, Goh et al. (2007) selectively isolated object and background scene-processing regions in young and old, Westerners and East Asians (Fig. 5b).

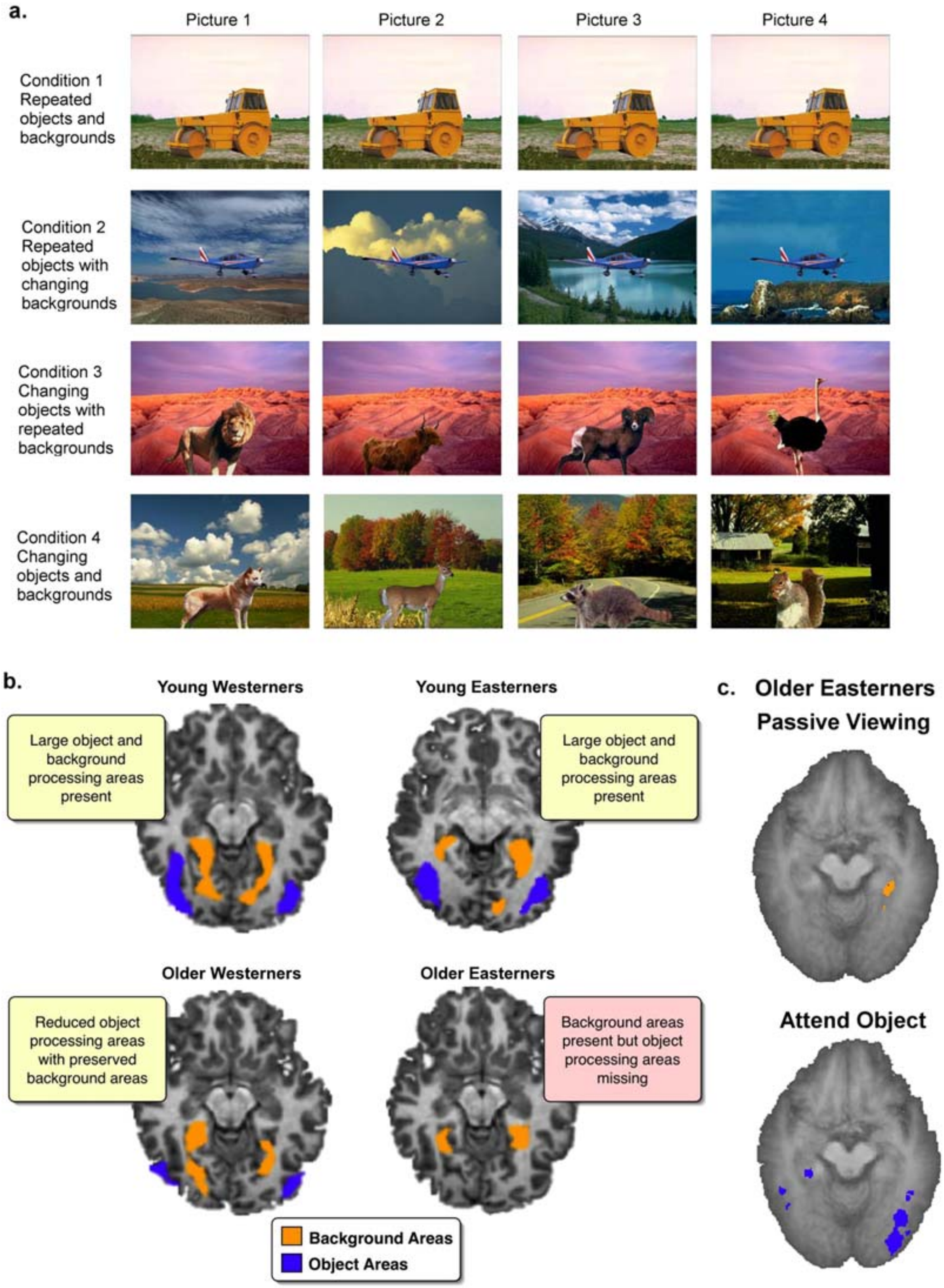

Fig. 5. (a) Sample quartet stimuli used in the fMR-A paradigm. Each quartet consisted of four pictures of objects within background scenes. Within each of the four quartet condition (rows), objects and scenes in the pictures were selectively repeated in order to isolate brain regions that were sensitive to the either object repetition or background scene repetition (adapted with permission from Goh et al., 2007). (b) Ventral visual regions involved in object and background processing were dissociated using the fMR-A paradigm in young and older, Westerners and Easterners as they passively viewed objects within background scenes (adapted with permission from Goh et al., 2007). (c) Object processing was not observed in older Easterners during the passive viewing task, but was restored when they were instructed to attend to objects (adapted with permission from Chee et al., 2006).

Importantly, data were acquired from participants within their home countries (Singapore and United States) using two magnets for which comparability had been examined (Sutton et al., 2008). The results showed that while background processing responses to repeated scenes in the parahippocampal regions was similar across all four groups, older East Asians showed significantly reduced object-processing activity in the lateral occipital regions. That is, older East Asians did not show adaptation in the lateral occipital regions when objects were repeated amidst changing background scenes. This finding was consistent with the notion of a cultural bias to engage more in object processing in Westerners compared to East Asians that was more evident in older adults than younger adults, possibly due to an interaction with a reduction of available attentional resources with age.

In a confirmatory follow-up of the postulate regarding attentional resource reduction in aging, a subset of the older adult East Asians who were tested in the previous study were tested again with the same stimulus presentation paradigm but with a modified instruction to attend to objects within the adaptation design regardless of the background scene repetition or change. In this study, object-processing activity in the lateral occipital region of older adult East Asians was restored (Chee et al., 2006; Fig. 5c). This suggests that the lack of object processing in older East Asians in the original study was due to a failure to attend to the objects, rather than due to a fundamental inability of the ventral visual cortex to process objects, since the effect was easily modulated by directing attention to the objects. Indeed, attentional control has been shown to modulate adaptation effects in other visual processing and attention studies (Henson et al., 2002; Yi et al., 2006).

Recently, Jenkins et al. (in press) also extended the fMR-A paradigm to investigate the effect of object and scene congruence on cultural differences in ventral visual activity. In that study, similar quartets of pictures were used as in Goh et al. (2004). In Jenkins et al. (in press), however, some of the quartets consisted of pictures with objects that were possible but highly unlikely (incongruent) with respect to the background scenes (e.g., a cow in a kitchen). This manipulation tapped into more semantic processing of relationships between visual components and evaluated whether cultural differences in attention to such contextual congruence would affect ventral visual activity. In line with greater sensitivity to contextual information in East Asians, the results showed that East Asians had greater adaptation in the lateral occipital regions when viewing incongruent compared to incongruent pictures. Westerners, however, did not show significant differences in adaptation responses as a function of congruence. This finding suggests that East Asians were more sensitive to the relationship between objects and scenes and engaged greater attention to the object that is incongruent to the scene, whereas Westerners may have focused on the objects more equally regardless of the congruence of the scene. This interesting application of the fMR-A paradigm suggests that cultural differences in ventral visual function are not only limited to attentional differences to objects and scenes separately, but also reflect cultural differences in processing of more semantic relationships between objects and the contextual scenes in which they occur. This is the first culture neuroimaging study to demonstrate semantic processing differences across culture that appears to affect ventral visual function. Nevertheless, cultural differences in processing semantic relationships between visual items have been previously demonstrated in behavioral studies (Chiu, 1972; Ji et al., 2004; Norenzayan et al., 2002) and probably do have some effect on processing at the ventral visual level, as these findings show.

In addition to these ventral visual cultural differences, at least one other neuroimaging study has found cultural differences in frontal and parietal regions when participants were confronted with a visual judgment task. Hedden et al. (2008) demonstrated that greater activity in the parietal regions was engaged when Western and East Asian participants were instructed to perform the Frame-Line Test mentioned earlier (Kitayama et al., 2003) when using the version of the task that was incompatible with their cultural

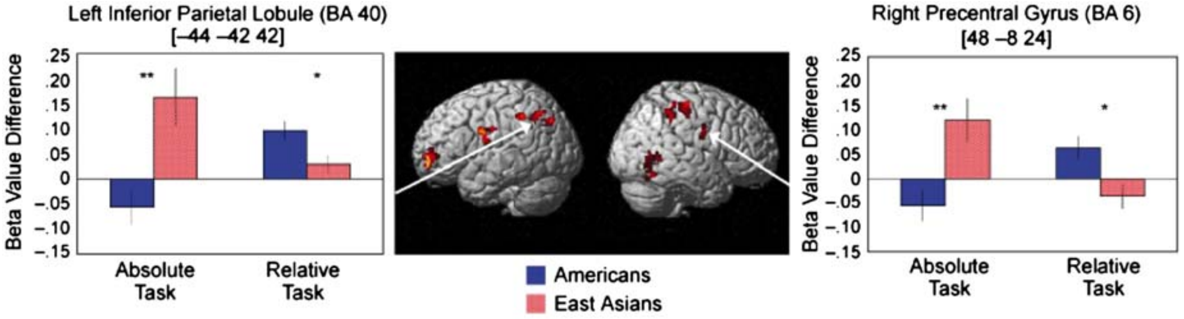

Fig. 6. Functional activity in the frontal and parietal regions when Westerners and Easterners perform the Frame-Line Test using absolute and relative judgments. Participants engaged greater activity when performing the task using culturally non-preferred modes of judgment (adapted with permission from Hedden et al., 2008).

biases. Specifically, East Asians engaged greater fronto-parietal activity than Westerners when making line-length judgments that required processing of the absolute length regardless of contextual square frame size (Fig. 6). In contrast, Westerners engaged greater fronto-parietal activity compared to East Asians during relative judgments that required contextual integration. Thus, although individuals from both groups were able to perform either task, indicating that cultural biases are not rigid or insurmountable, there was a neural cost associated with performing the culturally incompatible task. These findings are consistent again with a greater contextual-bias in East Asians and a more object-focused bias in Westerners, and suggest that the source of these biases may relate to top–down processes in these executive functioning regions that is modulated by cultural experiences. Interestingly, no culture differences were observed in the lower-level visual regions in this study or other studies reported. However, it is possible that primary visual areas are also affected by cultural experiences but the critical studies that demonstrate such differences have yet to be done. There is clear evidence that even sensory areas can reorganize as a result of experience (e.g., auditory or visual cortex reorganizes in blind and deaf subjects), so it is possible (but by no means certain) that culture could sculpt activation patterns in these areas.

Aging and cultural differences in ventral visual function

The impact of age on culture effects is of considerable interest, as older adults have sustained exposure to culture experiences that shape neurocognitive function (Alwin, 2008; Baltes et al., 2006; Park, 2008; Park and Gutchess, 2002; Park et al., 1999; Reuter-Lorenz and Mikels, 2006). At the same time that experience within the culture is increasing with age, neurocognitive function is declining. Aging is associated with multiple neural changes involving both brain structure and function (Dennis and Cabeza, 2008; Goh and Park, in press; Park and Reuter-Lorenz, 2009; Park and Goh, in press; Raz et al., 2005). In general, the aging adult brain declines in terms of neurotransmitter activity, cortical volume and thickness, and white-matter integrity, and shows increased frontal functional activity with reduced posterior activity such as in the hippocampus and occipital regions. To the extent that such biological age-related changes are dominant, neural activations associated with culture should become less distinctive and more similar as people age (neurobiological leveling hypothesis proposed by Park et al., 1999). If, however, cultural experience is the dominant force in shaping the aging brain, culture effects will get stronger with age.

To date, we are aware of only one neuroimaging study that has jointly examined the effects of aging and culture (Goh et al., 2007). This study, described earlier in this paper, showed that compared to the other groups, older adult East Asians had reduced object-processing activity in the ventral visual regions, namely the LOC. This reduction was not observed in young East Asians and was modulated by attentional processes. This finding suggests that culture effects were accentuated with prolonged cultural experience with older adult East Asians being even more susceptible to their cultural bias for contextual processing than young East Asians, and older adult Westerners showing a maintained bias for object processing as young Westerners. In contrast to this finding of accentuated culture effects with age, the most recent data from our lab (see abstract: Goh et al., 2008) indicated that aging is associated with reduced ventral visual specialization similarly in both cultural groups. It is possible that in this latter study (Goh et al., 2008), the blocked fMRI design with a passive viewing task may have been less sensitive to cultural differences in attentional processing, compared to the fMR-A paradigm used in Goh et al. (2007) in which objects and scenes were dynamically changing. Thus, more work on culture differences in neural structure and function is warranted to uncover what areas of neurocognitive function are most affected by environment, and what patterns of neural aging observed in Western samples are universal phenomena. Universality of findings across cultural groups is generally assumed by most researchers but as the present discussion suggests, it is entirely possible that some neural activity is modulated more by cultural experiences or other sustained experiences.

Conclusion

Culture represents a consistent set of experiences across one's lifetime that plays a role in shaping cognition and neural function. The effects of culture on cognition are of great importance in understanding the modifiability and plasticity associated with fundamental neurocognitive operations. The findings we have reviewed demonstrate that the ventral visual cortex in both Westerners and East Asians are organized in broadly similar ways with object processing in the lateral occipital and fusiform regions and contextual scene processing in the medial ventral visual regions including the parahippocampal and lingual regions. The findings also demonstrate that in both cultures, aging similarly leads to reductions in the level of ventral visual selectivity of neural responses to distinct visual categories. Despite these consistent global effects on the visual brain, culture operates in a subtle but specific manner, biasing ventral visual processes that reflect greater object processing in Westerners and greater context processing in East Asians. These biases are evident in localized brain regions and are also subject to changes with respect to different task requirements. Critically, the neuroimaging findings are highly consistent with the behavioral and eye-tracking findings on cultural differences in visual perception and attention showing analytic and holistic processing in Westerners and East Asians, respectively. At the very least, these findings point to a need to consider the role that culture plays in sculpting perception and some aspects of visual experience. The data presented suggest that the assumption of the invariance of cognitive processes across groups of individuals has to be objectively reevaluated.

An important, and relatively less studied, aspect of cultural neuroscience is the incorporation of structural brain data as a potential source of information regarding how visual stimuli is represented the minute it enters the brain. Structural brain organization sets a limit on how the system functions and may provide insight as to the underlying mechanisms and representations. Studies have shown that external experience does have bearing on specific brain structures (Boyke et al., 2008; Maguire et al., 2003). Some other studies have linked cultural differences to structural changes in the brain neuro-architecture as well (Green et al., 2007; Kochunov et al., 2003; Zilles et al., 2001). The findings, however, are less consistent and more data is needed. We propose that the same principles that underlie studies of neuroplasticity in brain structure due to unique and sustained learning or other experiences should be applied to studies of differences in brain structures that might be due to culture.

We emphasize that the evidence cultural differences in the visual brain presented here arises from differences in experiences and learning over the lifespan (Nisbett et al., 2001; Nisbett, 2003; Nisbett and Miyamoto, 2005; Park, 2008; Park and Gutchess, 2002; Park et al., 1999). Nevertheless, we readily acknowledge that biological differences between East Asians and Westerners are also a possible source of the differences observed in the imaging data and that a great deal more work is needed that systematically studies all potential factors affecting neurocognitive function. To the extent that neural differences between cultural groups are attributed to experience, it is important to identify the specific sources within each cultural environment that controls the effects and to study groups of individuals that are ethnically similar but who have not had these experiences to be certain of causal mechanisms. For example, one might study East Asians raised in Western environments or adopted into Western homes to parse out the effects of biology from culture. Considering the effects of cultural saturation which occurs in aged individuals also provides a novel way to approach how experiences can shape neural structures and function, providing a window into both the potential for plasticity within the neurocognitive system as well as the constraints conferred by biological aging. In sum, while much more cross-cultural imaging data are needed, the existing studies consistently reveal Western and East Asian cultural biases operating in the visual brain. Future culture imaging studies should investigate more specific mechanisms of these cultural biases as well as consider the joint effects of biological and experiential factors in determining neural development and function over the lifespan.

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CHAPTER 8

Neuropsychological assessment of African children: evidence for a universal brain/behavior omnibus within a coconstructivist paradigm

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Abstract: Cross-cultural neuropsychology with African and American children provides evidence of consistent deficit patterns in attention, working memory, and learning in children at risk from disease affecting brain function by means of similar pathophysiologic mechanisms (e.g., cerebral malaria (CM) and sickle-cell disease (SCD); HIV in African and American children). These brain–behavior disease processes are also modified in a consistent manner cross-culturally by quality of developmental milieu and caregiving. We then present findings from the pioneering use of computerized cognitive rehabilitation therapy (CCRT) with Ugandan children surviving CM and with HIV. This neuropsychological evidence that CCRT enhances positive brain plasticity in a consistent manner across cultures supports the ‘‘coconstructive’’ paradigm (Li, 2003), since plasticity across the life span is the hallmark of this approach.

Coconstructivism is a holistic multi-dimensional approach that emphasizes reciprocal biocultural influences across the life span. It also emphasizes the reciprocal interaction of culture and the genome in shaping brain/mind at multiple levels: neurobiological, cognitively, behavioral, and sociocultural (Li, 2003). Cross-cultural neuropsychology in healthy and diseased brains, brain imaging technologies, and genomic research can triangulate the manner in which a universal brain/behavior omnibus drives plasticity across the life span. As such, the further scientific characterization of the brain/behavior omnibus can provide the vital lynchpin between biology and culture in Li's coconstructive paradigm, revolutionizing our understanding of intelligence and culture.

Keywords: neuropsychology; Africa; children; brain; intelligence; culture; malaria; HIV

Four models on the relationship between cognitive ability and culture

In his 2004 Presidential Address to the American Psychological Association, Sternberg (2004) noted four different models for the cross-cultural measurement of intelligence. The first model proposes that the nature of intelligence is universal and that

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the same measure can consistently gauge intelligence as that instrument is adapted across cultures. The second model Sternberg described also is one in which the same measure can be used to assess intelligence across cultures. However, that tool may actually be measuring different underlying ability areas, given the possibility that individuals from different cultures may use diverse skills and approaches in arriving at the same correct response for a given task.

The third approach, and the one that Sternberg favors, proposes that the nature of intelligence is universal across cultures. However, the manner in which it is measured must be derived from within, and appropriate to the cultural context (Sternberg and Grigorenko, 2002). The fourth model is one in which both the nature of intelligence and the best means of measuring it are specific to the particular cultural context under investigation and arise in ecologically diverse, adaptive and unique ways. This approach tends to maintain the weakest view of a universal basis to specific cognitive skills. Instead, it emphasizes the impact of ecological adaptation on a culturally specific cognitive ability profile.

The coconstructivist approach to biocultural interactionism

In recent decades, Sternberg's fourth model, that of an emphasis on ecological adaptation in cognitive ability, was predominant within cross-cultural psychology (Rogoff and Chavajay, 1995). However, with the sequencing of the human genome and the accessibility of brain imaging technologies through MRI and functional MRI, the pendulum has now swung again toward genetic and brain determinism (Moore, 2002). Li (2003) has proposed a more holistic and inclusive paradigm, reviewing the reemergence of what he calls a "coconstructive" approach to the nature/nurture dichotomy. This approach emphasizes bidirectional reciprocal biocultural plasticity across the life span as the basis for cognitive tendencies and abilities. It also emphasizes the reciprocal interaction of culture and the genome in shaping brain/mind at multiple levels: neurobiological, cognitive, behavioral, and sociocultural (Li, 2003).

The research reviewed in this chapter draws mostly from the neuropsychological assessment of African children surviving cerebral malaria (CM) and with HIV. We use this work to illustrate how cross-cultural neuropsychology with African children can be illustrative of Li's coconstructivist paradigm. The studies we review neuropsychologically assess the impact of infectious disease and its treatment in the African context. These studies were not designed to broadly address all the major domains and levels of Li's coconstructivist paradigm. Nonetheless, we believe that the cross-cultural neuropsychological assessment of brain-injured and brain-healthy African children provides new methodological vantage points for the coconstructivism. These vantage points can further describe, clarify, and enrich our understanding of the inner-workings of coconstructivism. In fact, evidence from this work leads us to propose a new construct, that of a brain/behavior "omnibus," that we believe can enhance the coconstructivist approach.

Defining the construct of a brain/behavior omnibus

An omnibus is a framework that relates to or provides for many things at once. During the era of minicomputers in the 1970s, the omnibus was the foundational platform comprised of slotted places where the various computer circuit cards could be installed within the metallic box and display panel of the computer. In this review, the notion of a foundational platform as expressed by the term "omnibus" is very useful, although we are not likening the human brain to a computer or using the computer as a metaphor for such. We use the term "omnibus" as a metaphor for the manner in which bidirectional biocultural interactionism can shape plasticity across the life span, specific to the ecological needs of a given cultural context. This is consistent with a coconstructivist approach (Li, 2003), and can revolutionize our understanding of intelligence and culture.

The term "omnibus" is appropriate primarily because we do not wish to suggest that there exists a simple one-to-one brain area-to-behavior relationship for more universal and foundational cognitive ability domains such as attention, memory, language, or executive function. A given neuropsychological or cognitive ability is likely mediated by brain systems that involve integration at multiple levels, and this is consistent with our earlier definition of omnibus. We propose that the brain/behavior omnibus is the neuroscientific basis of biological and behavior plasticity across the life span. It is derived in the human genome and universal in nature. Because of this the omnibus is a strategic interface for the reciprocal interaction between the biological and cultural in shaping cognition. As the omnibus is driven by the cultural context in the molding of brain and cognition, it provides the lynchpin between biology and culture in Li's coconstructivism.

How "omnibus" empowers a coconstructivist paradigm

In terms of Sternberg's classification of various approaches to understanding the relationship between intelligence and culture, the brain/behavior omnibus can provide a bridge between cognitive neuroscience and an ecological psychology approach. We use cross-cultural neuropsychology research with at-risk African children to describe some of the major features of the omnibus. Our characterization of the brain/behavior omnibus is derived from studies that have used neuropsychological tests to evaluate brain injury from CM and from HIV in sub-Sahara Africa children. We also compare these findings to those from studies of American children with sickle-cell disease (SCD) and HIV as a means of identifying similarities in the brain pathogenesis of these diseases across cultures. We then interpret the more robust cross-cultural brain/behavior consistencies in light of Li's (2003) coconstructivist paradigm.

We also present experimental evidence from our recent efforts in the computerized cognitive rehabilitation therapy (CCRT) of Ugandan children surviving CM and children with HIV. Neuropsychological improvements from CCRT intervention provide documentation for this universal brain/behavior foundation across cultural contexts. Assessing the neuropsychological gains from CCRT across cultures provides a rigorous methodology for characterizing the omnibus. Neuropsychologically characterizing the omnibus basis of plasticity can also be enhanced by using Sternberg's "dynamic testing" approach. This approach evaluates improvement across repeated assessments in response to teaching the child the skills for such test items during the course of assessment.

We believe that both neuropsychological gains from CCRT and Sternberg's dynamic testing approach are sensitive to ways in which a brain/behavior omnibus is compromised as a result of poverty and infectious disease in African children. Because of this sensitivity, these approaches can reveal the more foundational features of brain/mind plasticity. In so doing, these approaches can prove strategic in enabling a coconstructivist paradigm to clarify and define its principles of reciprocal biocultural interactionism. This is because CCRT gains and dynamic approaches of assessment findings are derived from neuroplasticity, which is a hallmark of coconstructivism (Li, 2003). Therefore, they are more sensitive and consistent in characterizing cognitive ability across cultures, especially as such abilities relate to the integrity of brain/behavior function for brain-injured African children.

To conclude, we believe that CCRT gains analysis and Sternberg's dynamic measurement strategies in the context of cross-cultural neuropsychology will prove strategic in the advance of the coconstructivist paradigm. This will be especially true as these measurement techniques are complemented by brain imaging and genomic technologies, which are becoming more accessible in the developing world. In combination, these methodologies will describe how risk and resiliency factors mold cognition in consistent ways amidst a broad array of cultures, and against the backdrop of poverty and deprivation in human development. Such evidence will support and strengthen the power of a coconstructivist paradigm as a way of superseding Sternberg's four basic approaches to the nature/nurture conflict as reflected in the intelligence and culture debate.

The development of the K-ABC and its cross-cultural adaptability

In our neuropsychological assessment of African children surviving CM and children with HIV, we have primarily used the Kaufman Assessment Battery for Children (K-ABC). For consistency sake, we have also focused mostly on studies using the K-ABC as we consider findings from the study of American children with HIV or with SCD in our comparative review. It is therefore helpful at this point to explain our choice of a western-based cognitive assessment battery in the cross-cultural neuropsychological study of the impact of infectious diseases on brain/behavior development in African children. We have continued to use the K-ABC as our principal cognitive ability assessment because of its cross-cultural adaptability and proven sensitivity to even the more subtle effects of brain/behavior compromise from poverty and from disease in the African context (Boivin and Giordani, 1993; Boivin et al., 1993, 1995a, b, 1996b).

The cross-cultural adaptability of the K-ABC stems partly from the fact that it was designed to be appropriate for use with children not fluent in English. In both the 1st (Kaufman and Kaufman, 1983) and 2nd (Kaufman and Kaufman, 2004) editions of the K-ABC cognitive assessment battery, the authors sought to develop an assessment instrument that could clearly separate the Cattell–Horn distinction of acquired factual knowledge (crystallized intelligence) from the ability to solve unfamiliar problems (fluid intelligence) (Cattell, 1968; Horn and Cattell, 1966). Furthermore, within the subtests of fluid intelligence, an attempt was made to distinguish between simultaneous and sequential cognitive processing abilities (Das et al., 1979).

This distinction between the cognitive ability domains of simultaneous and sequential processing has been tested across cultural settings, and the results suggest that this dichotomy is a robust one. It remained intact when tested among rural Congolese children through factor analysis (Giordani et al., 1996). A meta-analysis of K-ABC validation studies has supported further the factor integrity of the sequential processing versus simultaneous processing distinction across multiple cultural contexts (Ochieng, 2003). More recently, the factor integrity of the 2nd edition of the K-ABC was also maintained in Ugandan children who have survived CM (Bangirana et al., 2009b).

Sensitivity of the K-ABC to proximal CNS effects and cognition

The K-ABC has a variety of subscales that measure both auditory and visual-spatial working memory (Kaufman and Kaufman, 1983, 2004). Boivin and colleagues have used the K-ABC to evaluate the cognitive impact of CNS infections prevalent among children in sub-Sahara Africa. These include malaria and the more indirect effects of intestinal parasite infection compounded by nutritional deficiencies (Boivin and Giordani, 1993; Boivin et al., 1993). The K-ABC has been used successfully in a variety of cross-cultural research settings by Boivin with Senegalese (Boivin, 2002) and Ugandan children surviving CM (Boivin et al., 2007; John et al., 2008a), children from DR Congo with HIV (Boivin et al., 1995b), and Ugandan school-age children with HIV (Bagenda et al., 2006).

Persisting neuropsychological impairment from cerebral malaria in Ugandan children

CM is a life-threatening form of *P. falciparum* complicated malarial illness characterized by coma and often accompanied by seizures and other neurological signs (WHO, 2000). Holding and colleagues found that children with a history of CM did significantly more poorly on K-ABC Sequential Processing (working memory) than did the mild or moderate malaria groups (Holding et al., 1999, 2004). The severe malaria group also did significantly more poorly on the visual search test (an attention task) and on pegboard (a fine motor task). For the Kenyan children surviving CM, schooling served as a buffer against persisting cognitive sequelae (Holding et al., 2004).

Boivin (2002) used the K-ABC and the Test of Variables of Attention (TOVA; www.tovatest.com) to evaluate Senegalese children who had survived CM. He found that children surviving CM did significantly more poorly on K-ABC global measures of working memory and visual-spatial processing. Boivin also observed that Senegalese children with a history of CM performed more poorly on a computerized measure of vigilance attention (TOVA) in comparison with children without a history of CM.

More recently, Boivin and colleagues evaluated the neurocognitive and neurologic sequelae of CM in a prospective study design with school-age Ugandan children (Boivin et al., 2007; John et al., 2008a). Neuropsychological and neurologic exams were completed at hospital discharge (0 months), and post-discharge at 3, 6, and 24 months. Forty-four school-age CM children followed through 2 years post illness were compared to a group of 52 children, recruited as outpatients at a malaria clinic (uncomplicated malaria or UM group), and 92 community control (CC) children without a history of CM or other brain injury who were recruited from the homes of the UM and CM children. Using the same measures used by Boivin in Senegal to study the neuropsychological effects of CM retrospectively (Boivin, 2002), Boivin, John, and colleagues observed that children had significantly lower attention ability throughout the 2-year period (Fig. 1, bottom left graph).

Ugandan children surviving CM had lower working memory (K-ABC Sequential Processing; top left graph in Fig. 1), but not significantly so by 2 years. Visual-spatial processing did not significantly differ among the groups between 3 months and 2 years (K-ABC Simultaneous Processing; top right graph in Fig. 1). Tactile-based learning on the Tactual performance Test (TPT) was initially slower, but did not differ at 2 years (bottom right graph in Fig. 1, top group). Overall, Ugandan children surviving CM have persisting significantly poorer levels of attention than their nonmalarial and uncomplicated malarial counterparts (Boivin et al., 2007; John et al., 2008a).

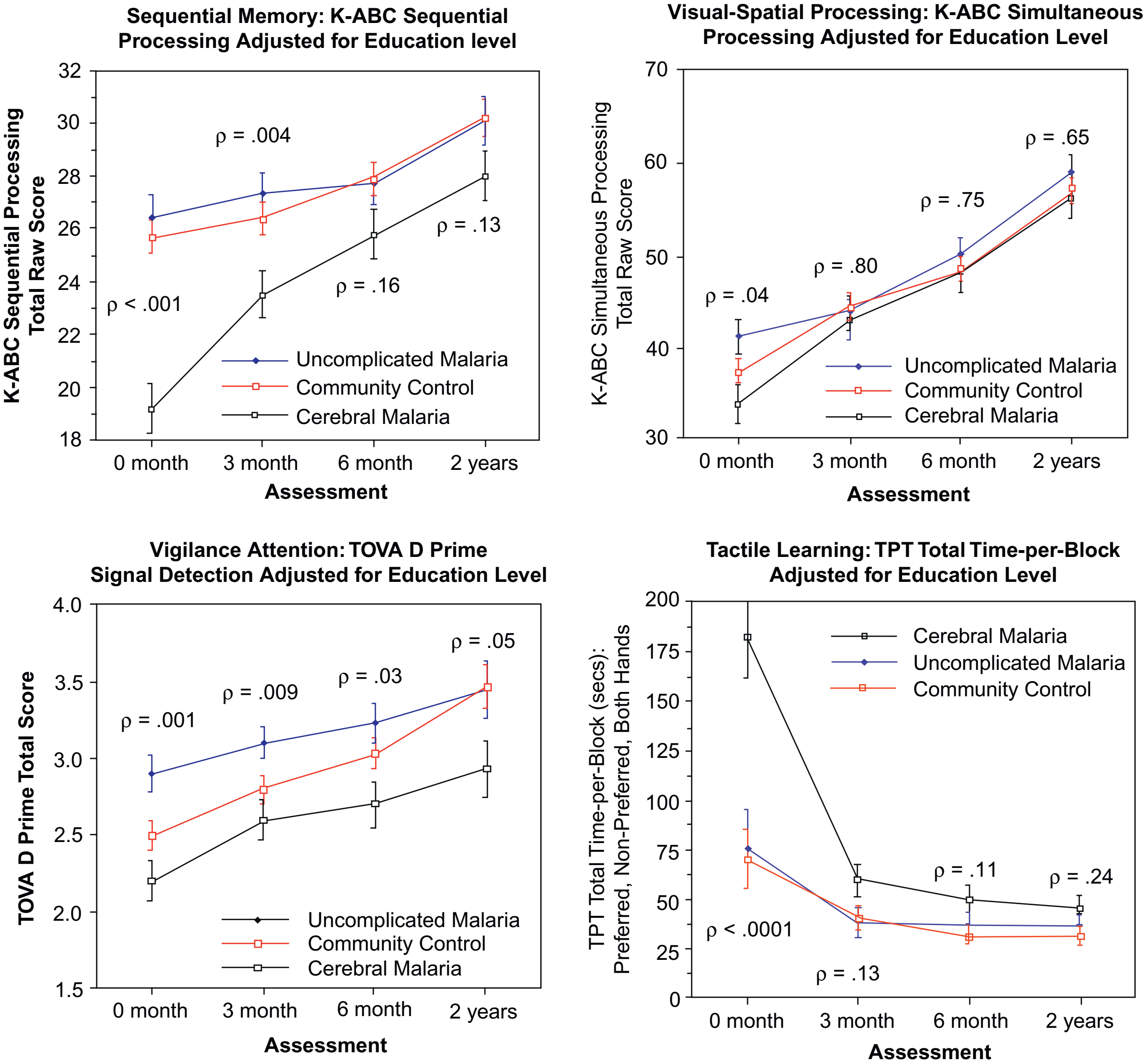
Sensitivity of the attention domain to brain injury in children

In the first published prospective studies of the neuropsychological effects of pediatric CM, the most persistent and significant deficits were those related to vigilance attention (Boivin et al., 2007; John et al., 2008a). Attention is a fragile component of cognitive function and adaptation and is vulnerable to almost any insult to CNS integrity. This appears to be the case whether CNS damage is virally induced, the result of neurotoxic exposure, or the result of head trauma and injury (Connolly and Kvalsvig, 1993). Boivin and Giordani (1995) concluded that one of the most pervasive signs of chronic sub-acute lead exposure in animal or human studies is attention problems (Boivin and Giordani, 1995). This is true even at exposure levels where IQ deficits and neurological soft signs cannot be clearly documented.

Consequently, neuropsychology research in the developing world has identified attention as one of the neuropsychological functions that is most clearly affected by CNS disease (Schmidt et al., 1994). Boivin and colleagues used the TOVA to document the sensitivity of attention testing to neuropsychological integrity in both urban and rural children in Laos (Boivin et al., 1996a) and in sub-Sahara Africa (Boivin, 2002; Boivin et al., 2007; John et al., 2008a). Attention processes are very sensitive to even milder forms of brain/behavior compromise and brain injury. Therefore, the cross-cultural neuropsychological assessment of attention, in response to injury and intervention, is critical in characterizing how the brain/behavior omnibus drives biocultural neuroplasticity across the life span.

The sensitivity of dynamic testing measures to brain/behavior integrity

Sternberg and Grigorenko (Sternberg, 2004; Sternberg and Grigorenko, 2002; Sternberg et al., 2002) have argued that dynamic assessment (measuring active learning ability across teaching sessions on a cognitive ability test) is more


Sequential Memory: K-ABC Sequential Processing Adjusted for Education level

Visual-Spatial Processing: K-ABC Simultaneous Processing Adjusted for Education Level

Vigilance Attention: TOVA D Prime Signal Detection Adjusted for Education Level

Tactile Learning: TPT Total Time-per-Block Adjusted for Education Level

Fig. 1. Cerebral malaria ($N = 44$), uncomplicated malaria ($N = 52$), and community control ($N = 92$) Ugandan children are compared at baseline, 3-month follow-up, 6-month follow-up, and 24-month follow-up (2 years). Baseline assessment was at hospital discharge for the cerebral malaria (CM) children, 1-week following outpatient treatment for the uncomplicated malaria (UM) children, and at enrollment for the community controls (CC), who were recruited from the households of the cerebral malaria and uncomplicated malaria children. The raw score means are plotted, adjusted for years of schooling. Each adjusted mean is presented with the standard error bar for that group. The ANCOVA significant probability (P) values are with each follow-up assessment between-group comparison. The Kaufman Assessment Battery for Children (K-ABC) global scale scores for Sequential Processing (upper left graph) and Simultaneous Processing (upper right graph) are presented. Attention was assessed using the Test of Variables of Attention (TOVA) visual test. The D prime signal detection scores from the TOVA are presented in the lower left graph. The lower right graph consists of the overall time per block averaged for all three trials of the Tactual Performance Test (TPT) (preferred hand, non-preferred hand, both hands). CM children had significantly lower attention ability throughout the 2-year period (bottom left graph, bottom group).

sensitive to brain/behavior integrity than traditional static (single time) assessments. In dynamic assessment, children are provided with feedback on their performance during testing and taught the skills necessary for a given type of test item. Subsequent improvements in cognitive performance in response to this teaching/learning dynamic are then noted across repeated assessment sessions. As such, dynamic assessment evaluates a higher level of positive biocultural plasticity, by evaluating the child's ability to adapt, learn, and improve from a feedback and learning environment (Sternberg and Grigorenko, 2002).

As evidence of the superiority of this approach in assessing overall cognitive ability, Sternberg and colleagues have demonstrated the enhanced sensitivity of dynamic measures in revealing the long-term impact of poverty on children in the developing world (Sternberg, 2004; Sternberg and Grigorenko, 2002; Sternberg et al., 2002). They also conducted cross-cultural assessment work in Tanzania, showing that conventional tests for working memory and for analogous reasoning (e.g., Raven's Progressive Matrices) will not adequately assess the full range of cognitive skills that children could potentially demonstrate. Dynamic testing in which feedback and instruction are provided to the children with these same cognitive ability measures, proved more sensitive to the impact of brain/behavior risk factors related to poverty and health for these children (Sternberg, 2004; Sternberg and Grigorenko, 2002; Sternberg et al., 2002).

We propose that Sternberg's dynamic measures of cognitive ability are especially sensitive to the neuroscientific and biocultural processes of negative and positive neuroplasticity. Because of this sensitivity to neuroplasticity in the developing brain, we propose that such measures provide another important avenue for characterizing a foundational brain/behavior omnibus. In addition to attention, biocultural plasticity as reflected in learning is another vital assessment domain in characterizing the brain/behavior omnibus. This is because when dynamic cognitive assessments are used to characterize neuroplasticity in children in a cross-cultural manner, universal foundational brain/behavior domains can emerge more clearly. Li (2003) emphasizes the fact that cognitive and behavioral plasticity are among the hallmarks of individual life span development and foundational to a coconstructivist approach. Therefore, learning ability is another critical dimension of the brain/behavior omnibus.

Brain plasticity and the use of computerized cognitive rehabilitation therapy

Mahncke et al. (2006a) define brain plasticity as the capacity for physical and functional brain change that can either be strengthened or degraded in a bidirectional manner, depending on the circumstances. Contrary to more traditional views that assume that the brain is hard-wired in early life (Woodruff-Pak, 1993), they argue that the human brain retains a neuroplastic capacity throughout the life span. Mahncke and colleagues demonstrated significant memory improvements for older adults with age-associated cognitive decline (Mahncke et al., 2006a, b; Smith et al., 2009), with non-impaired adults (Smith et al., 2009), and in a case study of HIV-related dementia (Spina et al., 2008).

Computerized cognitive rehabilitation therapy of Ugandan children surviving cerebral malaria

Boivin and colleagues used a CCRT intervention specifically designed for children (Captain's Log®, http://www.braintrain.com/) to enhance cognitive performance in Ugandan children surviving CM. These were children recruited about 3 years previously during acute illness who became part of a prospective follow-up study of the cognitive effects of CM (Boivin et al., 2007; John et al., 2008a). Thirty CM survivors were randomly selected to receive 16 sessions of CCRT training over an 8-week period, while the remaining 32 children served as a control group not receiving intervention.

Because the most prominent persisting cognitive deficit in the CM survivors was attention, the Captain's Log CCRT program was especially configured to emphasize attention skill in the training modules. In this intervention study, a computerized neuropsychological assessment screening battery (www.cogstate.com) was administered before and after the 8 weeks of training. Cogstate was designed as a neuropsychological screening tool with minimal practice effects and suitable in a repeated measures design for monitoring the benefits of treatment on neurocognitive disability (Darby et al., 2002). Our purpose in using Cogstate was to evaluate the benefits of CCRT intervention on attention, memory, and learning.

Using a neuropsychological screening test such as Cogstate to assess gains from CCRT is not a dynamic assessment approach in the manner described by Sternberg. This is because neuropsychologically assessing gains from before to after CCRT does not involve intentionally teaching children the skills necessary for doing the items as they complete them. However, Cogstate is a computer-based neuropsychological assessment that does provide immediate feedback throughout the assessment as to whether the child's response is correct or incorrect. Because of this and other features, Cogstate may be sensitive to learning and the neuroplastic benefits of CCRT on brain/behavior function.

In fact, the Ugandan CM survivors receiving CCRT had significantly greater gains on (1) speed on the Cogstate simple attention task for detection of the turning of playing cards; (2) efficiency on a visual-motor target chasing task; and (3) greater efficiency and reduced errors on a maze learning task. Figure 2 includes the box plot comparisons between CCRT and non-CCRT groups of Ugandan CM children on visual-motor target chasing (Groton Maze Chase, upper left graph) and Groton maze learning (upper right graph) (Bangirana et al., 2009a; Boivin et al., 2008). It is likely that the attention training emphasis from CCRT intervention contributed to significant improvements on Cogstate reaction time for the card turning task and on Groton target chasing and maze learning tasks. It should also be noted that even though CCRT has produced significant neuropsychological benefit in American and Swedish children with ADHD (Klingberg et al., 2005; Rabiner, 2008), these are the first such findings reported with African children.

The neuropsychological CCRT gains documented cross-culturally from these studies provide further experimental evidence for the importance of positive neural plasticity in the learning domain of a more universal brain/behavior omnibus. These findings also evidence the utility of cross-cultural neuropsychological assessment of CCRT gains as a useful methodology for exploring the mechanisms of positive neuroplasticity within Li's coconstructivist paradigm.

Cerebral malaria, negative neuroplasticity, and reduced CCRT neuropsychological benefit

Because children in the longitudinal study described above were enlisted into the study cohort during acute illness and hospitalization for CM, Boivin and colleagues were able to evaluate the predictive relationship between clinical measures of severity of illness and neuropsychological follow-up assessment. For example, lumbar puncture is routinely performed on CM children at hospitalization in order to rule out certain forms of meningitis and encephalitis as the cause for coma. In analyzing various cytokine levels within the cerebrospinal fluid (CSF), it was found that TNF-alpha level was negatively related to attention and working memory deficits in the CM cohort 6 months after illness (John et al., 2008b). We hypothesize that TNF-alpha may also be predictive of Cogstate performance in the CCRT study children, and are presently evaluating these findings.

John and colleagues have documented in this same Ugandan CM cohort that CM was associated with greater endothelial cell activation in the microvasculature, as compared to UM. This is evidenced by the fact that a propeptide called von Willebrand Factor (vWF) is highly predictive of CM illness severity in these children (Park et al., 2008). John, Boivin, and colleagues are presently evaluating the predictive sensitivity of vWF to CCRT training benefit on Cogstate performance in Ugandan CM children. They hypothesize that vWF will prove to be sensitive as a marker of severity of brain pathogenesis during acute CM illness because it has been shown that the endothelium is activated during severe malaria infection, mediating sequestration and subsequent

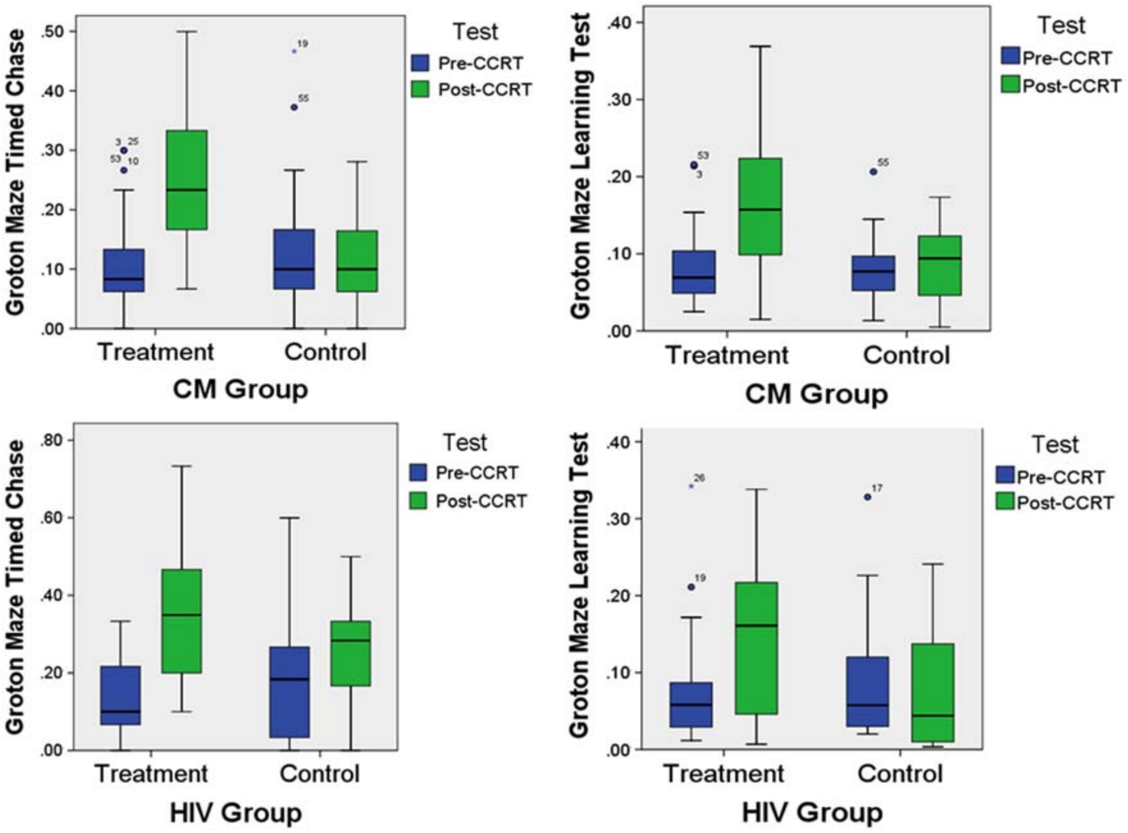


Fig. 2. Box plots depict correct moves per second on the Cogstate Groton maze target chase task (left graphs) and Groton maze learning task (right graphs). The upper pair of box plots is for the cerebral malaria Ugandan children, and the lower pair of box plots is for the Ugandan children with HIV. Each box plot compares the performance for children receiving Captain's Log computerized cognitive rehabilitation therapy (CCRT) and the control children not receiving CCRT. The median performance measure divides the box; while the upper boundary of the box corresponds to the 3rd quartile and the lower boundary corresponds to the 1st quartile. The minimum and maximum values extend as bars from the bottom and top of the box, while the outliers are plotted as data points. The dark box plots represent Groton maze performance before CCRT training and the lighter boxes represent performance at the end of the training period. CCRT intervention children (Treatment) displayed significant gains on Groton maze target chase and maze learning from before to after training; while the non-intervention (Control) children did not. This was the case for both the cerebral malaria survivors (upper box plots) and the children with HIV (lower box plots).

hypoxic tissue damage (de Mast et al., 2007; Hollestelle et al., 2006; Park et al., 2008).

Cross-cultural neuropsychological findings comparing sickle-cell disease to cerebral malaria

The cross-cultural consistency of deficit profiles for sickle-cell disease and cerebral malaria

Boivin (2002) proposed that the similar neuropsychological deficit profiles of CM and SCD result because both diseases involve a serious compromise of the ability of red blood cells to flow through the fine capillaries and arterioles of the deep structures and "watershed" regions of the brain vasculature. This is supported by MR imaging evidence from both disorders (Armstrong et al., 1996; Kugler et al., 1993). Furthermore, the most pervasive cognitive effects of SCD and CM are impairment on sustained attention tasks, visual-spatial and visual-motor integration and memory deficits, and executive function deficits as they relate to visual-spatial judgment and the higher-order cognitive sequencing of such information (Armstrong et al., 1996; Boivin, 2002; Kihara et al., 2006).

The neuropsychological and cognitive sequelae associated with CM in children are also consistent with MRI imaging studies with SCD asymptomatic children. SCD can injure the brain through acute hypoxic-ischemic effects that are similar in many respects to brain injury from CM (Hollestelle et al., 2006; Schnog et al., 2006). This is important because SCD has been both neuropsychologically evaluated and studied with the latest in brain imaging technologies in high-income countries. Furthermore, SCD and CM have similar neuropsychological deficit profiles, pointing to the utility of cross-cultural neuropsychology in revealing consistency in some features of the pathophysiological process with different disease groups across cultural contexts. Such findings evidence the utility of cross-cultural neuropsychology as an assessment tool with Li's coconstructivist approach.

For example, SCD children evidence cerebrovascular insufficiency syndrome in the microvasculature demonstrated by micro-infarcts in the deep white matter of the frontal lobes and basal ganglia (Kral et al., 2001, 2003). Sub-clinical SCD children demonstrated subtle yet consistent differences compared to normal controls in sustained attention. Kral et al. (2001) in their comprehensive review of the SCD neuropsychological literature note that SCD children also generally score lower on global measures of fluid intelligence, even in the absence of stroke or other MRI abnormalities (Armstrong et al., 1996; Hollestelle et al., 2006; Kugler et al., 1993; Schnog et al., 2006). This is consistent with the finding that CM children score significantly lower on the global cognitive ability indicators of K-ABC Sequential and Simultaneous Processing (Boivin, 2002).

MRI and neurocognitive impairment findings with SCD children also correspond to the CM imaging evidence. T1- and T2-weighted MR images with SCD children reveal bilateral lucanae and leukoencephalopathy in the centrum semiovale, paraventricular white matter, and frontal lobes (Steen et al., 2003a–d). Similar findings were obtained in the one available MR case study of pediatric CM (Gamanagatti and Kandpal, 2006). Furthermore, SCD children with MR abnormality were significantly below normal on Wechsler Verbal and Performance IQ (Steen et al., 2003c).

Furthermore, SCD contraction of these activated endothelial cells is mediated in their adhesive interactions with bridging molecules from the plasma such as vWF. In SCD, the release of vWF culminates in vasoocclusion and local tissue ischemia and very likely forms the pathognomonic basis of vasoocclusive crisis in the brain (Pathare et al., 2003). A similar brain pathophysiological mechanism mediated by vWF seems to be at work in CM (de Mast et al., 2007; Hollestelle et al., 2006; Park et al., 2008).

These cross-culturally robust brain/behavior relationships are consistent for two different diseases sharing a critical pathogenic feature (cerebrovascular hypoxic/ischemic effects on the centrum semiovale and paraventricular white matter). SCD children with lesions to these areas have more significant cognitive deficits compared to children without such lesions. In summary, the brain/behavior relationships for SCD correspond to those of CM, even though the clinical studies are based in entirely different cultural contexts. This conclusion supports the utility of cross-cultural neuropsychology in evidencing a universal brain/behavior foundation in developing children. The consistent and robust nature of the MRI and neuropsychological relationships for both SCD and CM also suggest that executive functions undergirding fluid intelligence are an important domain to consider for a universal brain/behavior omnibus. When complemented by brain imaging technologies, cross-cultural brain/behavior studies of disease affecting the CNS can be a powerful tool in characterizing the universal omnibus at the heart of neuroscientific plasticity within a coconstructivist paradigm.

Sensitivity of the working memory domain to HIV

The following pediatric HIV developmental and neuropsychological assessment literature documents consistent neuropsychological impairment trends in brain/behavior relationships. This is despite the use of different western-based standardized assessment measures in a variety of cultural contexts.

Furthermore, the neuroanatomical and neuroimmunological markers of disease progression relate directly to the specific neuropsychological deficits shown consistently across the different cultural contexts for this disease. This supports a robust and foundational neuroanatomical basis for the observed brain/behavior deficits from pediatric HIV.

To illustrate, the K-ABC has been used with HIV-positive Congolese children (Boivin et al., 1995b) and with Ugandan school-age children with HIV (Bagenda et al., 2006). The deficit profile for the K-ABC subtests is consistent with findings of earlier studies with HIV-infected American children (Belman et al., 1988; Diamond et al., 1987). Specifically, these studies have consistently reported significant deficits in K-ABC memory scales that pertain to both visual-spatial (hand movements, spatial memory) and auditory (number recall) working memory. Significant differences on motor development as compared to non-infected children also were found for HIV-positive children in Boivin et al. (1995b) for both toddlers and older children in separate studies, as also reported in neuropsychological studies with American children (Wachsler-Felder and Golden, 2002).

Sensitivity of the motor development domain to HIV

HIV-infected American children show impairments in motor development compared to non-infected children, using the Bayley scales (Blanchette et al., 2001, 2002). Furthermore, the extent of CT scan abnormalities for the infected children was associated with developmental delays, particularly for motor development. Specifically, HIV-infected children without clear CT abnormalities had scores that indicated mild neurodevelopmental delays, while HIV-infected children with CT abnormalities had scores that indicated significant delays.

Even HIV children scoring within the normal range for most of their cognitive ability domains still demonstrate subtle fine motor and motor strength impairments. This is also the case in children with deficits in visual-motor and visual-spatial processing that are associated with CT documented structural anomalies in the brain (Blanchette et al., 2002). Similar cognitive deficit findings have been observed with children with HIV in the DR Congo (Boivin et al., 1995b; Van Rie et al., 2008).

HIV effects on executive functioning in American and European children

Besides working memory and motor deficits mentioned above, neuropsychological testing has revealed executive function deficits even in neurologically and immunologically asymptomatic HIV-infected children (Bisiacchi et al., 2000). It has been proposed that visuo-motor skills may be the most affected cognitive area in relation to stage of disease, mode of transmission, and the children's living environment (Frank et al., 1997).

Using the McCarthy Scales of Children's Abilities, quantitative, verbal, and memory ability deficits also have been documented with infected children, particularly in those children with accompanying neurological impairment from the virus (Levenson et al., 1992). In addition, deficits pertaining to visual-spatial integrative ability and memory have been identified using the K-ABC (Belman, 1992; Belman et al., 1988; Boivin et al., 1995b; Diamond et al., 1987, 1990).

Using HIV to establish a universal basis to cognitive ability

Positive neuroplasticity and cognitive rehabilitation therapy: brain plasticity and functional loss in pediatric HIV

The neurocognitive deficits associated with pediatric HIV seem to reflect more diffuse processes, as opposed to focal CNS deficits (Angelini et al., 2000). In children with HIV, spatial memory ability is correlated with choline concentration in the hippocampus (Keller et al., 2004). If spatial memory impairment is mostly due to brain injury that is irreparable, then cognitive rehabilitation training will likely be of limited benefit. However, if one holds to the view that brain plasticity extends beyond early childhood, then there is greater hope that HIV-related brain injury can be effectively treated with cognitive rehabilitation training. This view is the basis of our CCRT study with Ugandan children with HIV (Boivin et al., 2008).

The neuropsychological benefit of CCRT for children with HIV

We have also completed a Captain's Log CCRT intervention study with 60 Ugandan children with HIV infection. Thirty-two of these children were randomly assigned to 5 weeks (twice weekly) of CCRT or to a no intervention group. The CCRT intervention group had significantly greater improvement than the controls for Cogstate card turn detection speed ($P = 0.03$) and greater efficiency in the Groton Maze Learning Task ($P = 0.02$) (Fig. 2 bottom right). There were also marginally significant gains on the Groton Maze Chase Task ($P = 0.06$) (Fig. 2 bottom left) (Boivin et al., 2008). We believe these findings to be very important because CCRT intervention has not been previously reported in African children so far as we are aware, and because of the robust and consistent nature of neuroplasticity benefit across two different disease groups in the Ugandan context. These benefits were mostly with respect to attention, which was the cognitive domain specifically targeted in the CCRT. The benefit then extending to maze learning, suggesting a positive neuroplasticity enhancement consistent with the model proposed by Mahncke et al. (2006a, b) and consistent with a coconstructive perspective.

CD8 and CD4 activation levels are significantly correlated with gains from CCRT on maze learning

For children with HIV receiving CCRT, improvements in maze learning from CCRT were significantly correlated with both CD8 ($r = 0.36$, $P = 0.03$, df = 29) and CD4 ($r = 0.38$, $P = 0.04$, df = 28) activation level (see Fig. 3). These correlations were not significant for the control group (no CCRT intervention) of children with

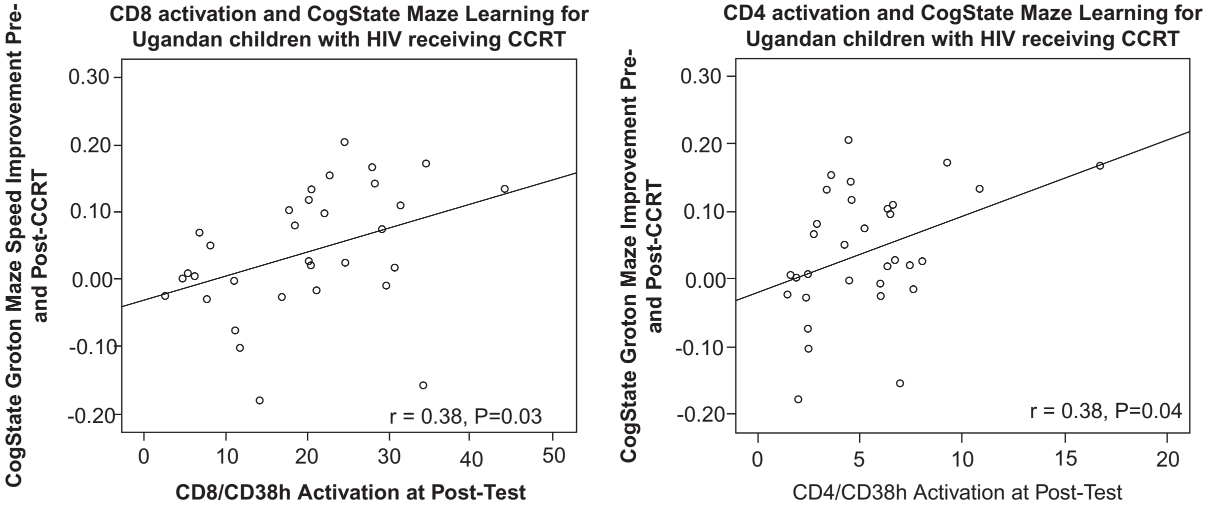


Fig. 3. For Ugandan children with HIV receiving 10 sessions (5 weeks) of Captain's Log computerized cognitive rehabilitation training (CCRT) ($N = 32$), performance gains on Cogstate Groton maze learning (pre- to post-training) are plotted as a function of serum CD8 (left scatterplot) and CD4 (right scatterplot) activation. CCRT maze learning performance gain is significantly related to both CD activation measures.

HIV. Also, CD8 and CD4 activation levels were not significantly correlated with pre-CCRT Cogstate performance measures.

Low blood CD8+ T-lymphocytes and high circulating monocytes are predictors of HIV-associated progressive encephalopathy in Spanish children (Sanchez-Ramon et al., 2003). These authors suggest that the suppression of HIV replication is dependent on CD8 lymphocytes, and that diminished response of these T cells is a reliable marker of the clinical neurologic emergence of progressive encephalopathy. Others have concluded through a meta-analysis that only virologic markers were significant predictors of cognitive impairment in children with HIV (Lindsey et al., 2000). Irrespective, the relationship between immunologic status of the HIV children and the degree of Cogstate learning benefit from CCRT intervention evidences the sensitivity and utility of learning-based measures of cognitive improvement that draw upon the brain's neuroplastic capacity.

Even if HIV children are clinically stable, there is progressive encephalopathy of this disease at the neuronal level (Okamoto et al., 2007). Therefore, it is medically and scientifically important to know if this relentless encephalopathy can be neurobiologically treated or cognitively remediated using CCRT. If so, then such cognitively based interventions are impacting brain/behavior omnibus function at a foundational level and doing so in a consistent manner across diverse environmental and cultural settings in support of a coconstructivist approach to understanding these processes.

Using quality of home environment to establish a universal basis to cognitive ability

Dissociating developmental effects of poverty from the CNS effects of malaria or HIV illness

A more universal brain/behavior foundation to cognitive ability might be further supported by neuropsychological measures that could differentiate between disease and environmental influences on cognitive performance in a consistent manner across cultures. Nutritional deficiencies, environmental deprivation, poor sanitation and hygiene, iron-deficiency and anemia, malaria, schistosomiasis, intestinal parasite infections, and diarrheal disease are just some of the chronic conditions afflicting sub-Saharan African children and dampening or impairing neuropsychological development and function (see Grantham-McGregor et al., 2007, for a recent review). However, for African children in resource-poor settings, it is difficult to disentangle the effects of such diseases from the long-term effects of poverty in shaping neuropsychological function. Boivin (2002) documented the importance of whether children were from a more impoverished rural or urban area as a modifying factor in the neuropsychological effects of CM. Likewise, education can be a buffering factor in the neuropsychological outcomes of severe malaria in Kenyan children (Holding et al., 2004).

Ninety-one percent of child HIV infections and 94% of child AIDS deaths occurred in Africa (Foster and Williamson, 2000). In these areas, family resources are strained by the environment and the disease. The cognitive development of HIV children may suffer from the direct CNS effects of the disease, as well as from the devastating effects on quality of developmental milieu from the loss of principal caregivers and other family members to the disease.

Non-infected children with infected parents or family members are also at greater risk from the poverty that may be further compounded by the economic hardship imposed by HIV illness in the family (Fair et al., 1995). Even in the absence of HIV infection for the child born to an infected mother, characteristics of the home environment for the infected parent(s) can significantly compromise the cognitive and behavioral development of the child over the long-term (Boivin et al., 1995b; Mellins et al., 1991; Van Rie et al., 2008).

Quality of home environment and caregiving as modifying factors in the neuropsychological evaluation of HIV

Quality of home environment and level of nutrition and physical development are especially predictive of the K-ABC Simultaneous Processing global scale (visual-spatial analysis and problem solving) in healthy children in the DR Congo (Boivin and Giordani, 1993; Boivin et al., 1993, 1995a) and in HIV children in the same area (Boivin et al., 1995b). However, Sternberg and Grigorenko believe that dynamic assessment (measuring active learning ability across teaching sessions on a cognitive performance task) is the best way to reveal the long-term impact of poverty on children in the developing world (Sternberg, 2004; Sternberg and Grigorenko, 2002; Sternberg et al., 2002). Even so, some tests such as the K-ABC Simultaneous Processing domain may have more dynamic features that are sensitive to neuroplasticity. These measures would then be sensitive to the more long-term effects of poverty, enrichment of developmental milieu, and quality of caregiving on neurocognitive development (Bangirana et al., 2009c).

For 43 HIV-infected American children between the ages of 2.5 and 12 years, quality of home environment mediated the relationship between socio-economic status (SES) and overall cognitive ability performance (Coscia et al., 2001). SES and quality of home environment were much more significantly related to IQ than degree of illness and health status for the children. Quality of home environment was defined by the organization of the environment, play materials, parental involvement, variety of stimulation, and parental attitudes toward the provision of a cognitively stimulating environment. Furthermore, the mediational role of quality of home environment was stronger for children who in a more advanced stage of illness from the disease as determined by health status and CD4 counts.

These findings were consistent with those in which 11 British HIV-positive children, aged 4–13 years, were assessed twice in a longitudinal assessment of cognitive, adaptive, and behavioral functioning. There was wide variability in the children's functioning, with some children displaying significant weaknesses in adaptive functioning and a high prevalence of behavioral and attention difficulties for the group as a whole. The authors suggested that poor SES conditions as well as social instability from the effects of the illness on the family were partly responsible for these adjustment and cognitive effects (Gosling et al., 2004).

The cross-cultural impact of quality of home environment for children with HIV in the above review of the literature provides evidence of the top-down directional impact of environmental context on neuroscientific plasticity. This is consistent with the biocultural interactionism of Li's coconstructive approach, and reveals yet another way in which cross-cultural neuropsychology can be methodologically useful within this paradigm. These finding also allude to the interaction between quality of developmental milieu and neuroscientific plasticity in the integrity of the brain/behavior omnibus.

Evidence for biogenetic arrays linked to attention

The technology for multivariate genetic analysis and quantitative trait loci (QTLs) through genetic microarray assessment in children continues to develop rapidly. Part of this advance involves genetic markers for neurodevelopmental risk factors that we believe could pertain to neuroscientific plasticity across the life span (e.g., apolipoprotein E on allele 4 or APOE4).

Because of the potential accessibility of this technology to specimens from even the most remote regions of Africa, biogenetic array analysis could provide another means of establishing the universal nature of neuropsychologically assessed brain/behavior attributes as they are linked to those genetic profiles in children (Plomin, 2004). Attention impairment is one of the principal persisting effects of CM. As reviewed by Plomin (2005), one important recent area of research illustrating this potential is multivariate linkage associative research between specific ADHD subtypes and the DRD4 and DAT candidate genes (Asherson, 2004; Todd et al., 2005; van der Meulen et al., 2005).

With the science of proteomics continuing to unravel the relationship between QTLs and the enzymatic and protein construction basis to the development and consolidation of neuronal networks in children, genetic psychology will be able to target the impact of pediatric illness and disease on cognitive ability domains that are both biogenetically and neuroscientifically differentiated. Furthermore, it will do so across a broad swath of differing cultural and environmental settings and ethnicities. Finally, it will be predicted by neuropsychological and brain imaging assessments at points further downstream in a child's cognitive ability development.

As evidenced by our preceding review of genomic research and attention in children, cross-cultural neuropsychology is complemented by genomic technologies. Together, they have great potential in clarifying the bottom-up nature of bidirectional biocultural interactionism within a coconstructivist paradigm. The addition of MRI and other brain imaging technologies, though less accessible in the developing world, adds yet another strategic manner to triangulate the role of a universal foundational brain/behavior omnibus in driving plasticity across the life span. Again, this will support and enhance a coconstructivist approach.

The use of MRI imaging with cross-cultural neuropsychology to study attention in Malawian children

As MRI brain imaging technologies become increasingly accessible for CM and HIV children in Africa, we will be able to document the brain–behavior pathways mediating attention, memory, and other cognitive deficits from CM and HIV. We hypothesize that the resulting observed brain/behavior relationships will be consistent with what has been documented in high-income countries, and will further support the notion of a universal brain/behavior omnibus.

To illustrate, Michigan State University has recently installed an MRI scanner at the central public hospital of Blantyre, Malawi. This scanner was donated by the General Electric Corporation, is being used clinically as well as for severe malaria research (Oswald, 2008). This scanner will be used to pioneer the systematic evaluation of the structural and dynamic effects of acute-phase pediatric severe malaria. When coupled with neuropsychological evaluation, it will be possible to evaluate the brain/behavior impact of CM on attention, memory, language, and other cognitive performance domains.

Dr. Semrud-Clikeman and colleagues have documented the differential impact of Ritalin on the caudate and anterior cingulate (AC) gyrus of children with ADHD, compared to non-medicated ADHD and non-ADHD children (Semrud-Clikeman et al., 2006). They have begun to evaluate these regions in Malawian children surviving CM. Figure 4 depicts the caudate (Image 1), AC cortex (Image 2) in a Malawian CM survivor. These regions, along with the posterior inferior vermis, significantly differ in volume when comparing Ritalin-naïve to treated ADHD American children (Bledsoe et al., 2009; Semrud-Clikeman et al., 2006). Semrud-Clikeman also observed significant relationships between right and left caudate volume and attention performance measures. Perhaps similar brain/behavior evaluations can be made for Malawian children receiving long-term interventions for ADHD symptoms acquired from CM, supporting the universal neuroscientific plasticity that is central to a brain/behavior omnibus.

Such findings may, at some time in the future, make possible the differential diagnosis of ADHD using something other than subjective behavior or symptom inventories (Willmott and Ponsford, 2009). If we can replicate Dr. Semrud-Clikeman's work in Malawian children with acquired attention problems from CM, and in those diagnosed with ADHD of unknown origin, this would argue for a more universal brain/behavior omnibus basis for defining the nature of ADHD. Such findings would also contradict the view that ADHD is mostly a culturally defined diagnosis, and would strengthen the bottom-up line of directionality for this neuroplastic domain within Li's coconstructivist approach.

A summary of the utility of omnibus as a modeling construct within coconstructivism

We have used evidence from the neuropsychological assessment of healthy and brain-injured African children to support the contention that

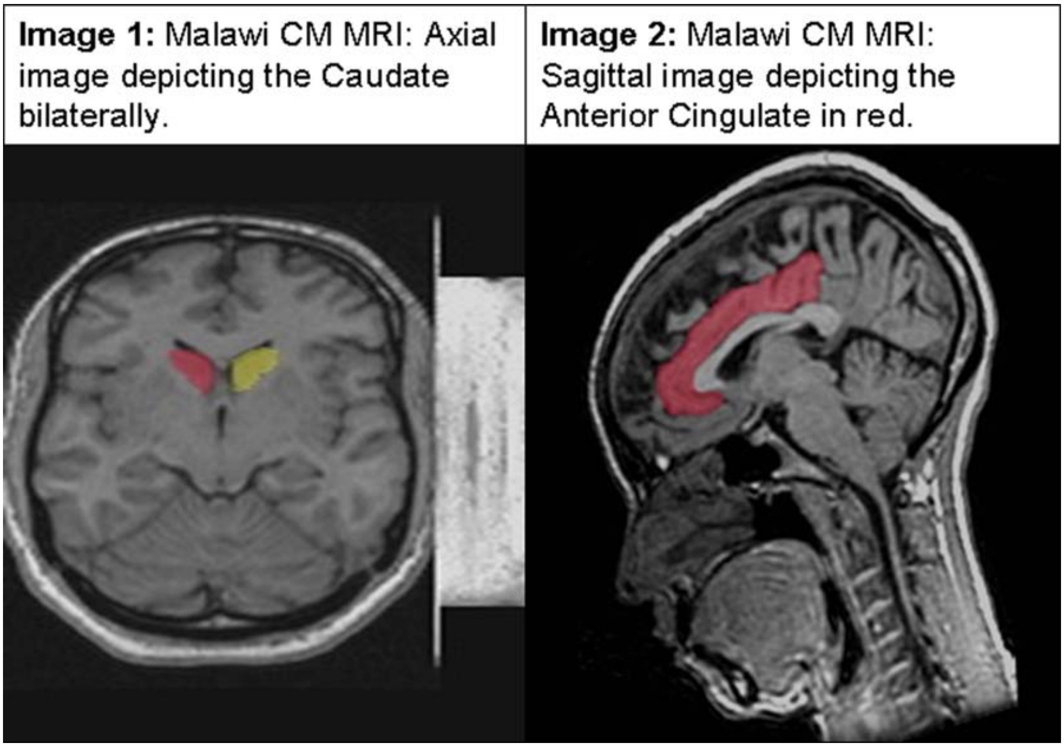


Fig. 4. MRI region of interest analysis is presented for a Malawian cerebral malaria survivor. This scan was performance by the only MRI scanner in Malawi, commissioned in June, 2008 by Michigan State University, Queen Elizabeth Central Hospital in Blantyre, and the Malawi Ministry of Health. The left image depicts the caudate bilaterally, while the right image depicts the anterior cingulate cortex. In volumetric analysis with American ADHD children, both regions have been significantly related to neuropsychological performance and improvements from treatment. Images provided by Jesse Bledsoe and Margaret Semrud-Clikeman at Michigan State University, and used with permission.

there is a universal basis to cognitive ability that lends itself to assessment, even with western-based tests such as the K-ABC. We proposed the metaphor of "omnibus" to might help us relate more universal foundational aspects of brain/behavior processes to more culturally specific cognitive abilities. In our review of cross-cultural neuropsychological research with African and American children with CM, SCD, and HIV, we concluded that such robust and more universal brain/behavior domains as attention, working memory, and other more executive functions emerge from the omnibus, which in turn drives plasticity across the life span. In the larger framework of coconstructivism, cross-cultural neuropsychology coupled with genomic and brain imaging technologies, can identify ways in which the brain/behavior omnibus is derived ultimately from what Li (2003) identified as genetic, neuronal, structural, and functional plasticity. It is this neuroscientific plasticity that is assessed by more dynamic forms of testing (Sternberg, 2004; Sternberg and Grigorenko, 2002) and by neuropsychological gains from CCRT intervention (Fig. 2). The omnibus driving this plasticity is affected by both CNS disease (proximal influences) and poverty (distal influences). It is also molded by the adaptive needs expressed within diverse ecological and cultural settings, in a manner consistent with the bidirectional biocultural emphasis of Li's coconstructivism.

To illustrate, Salthouse (2005) found in his analysis of two large neuropsychological datasets with adults that executive functioning performance mostly came down to reasoning and perceptual speed abilities (Salthouse, 2005).

This led him to question whether executive functioning alone actually represents a distinct process or domain. Instead, how the brain/behavior omnibus features of executive functioning are best defined or measured may depend on the manner in which a cultural context selects for specific cognitive skills, such as analogous reasoning or pattern recognition.

Other uses of cross-cultural neuropsychology across the life span in support of coconstructivism

Although the manner in which executive functioning is expressed and measured may differ from culture to culture, we would argue that there are basic omnibus processes that are universal and foundational to such abilities. A cross-cultural neuropsychological approach to the cognitive changes associated with aging has been revealing these types of foundational domains across the life span. We illustrate with examples below from the cross-cultural neuropsychological study of aging.

Research into the cognitive neuroscience of aging has been mostly conducted in western populations. However, as such research has extended into East Asian populations, it has identified those age-related neural changes that are persist across cultures, and are perhaps universal (Park and Gutchess, 2002). It has also revealed those that are specific to the particular experiences within a culture over time (Hedden et al., 2002). The cross-cultural application of brain imaging and behavior genomics and functional brain imaging technologies, to the cognitive neuroscience of aging, has further supported the coconstructivist approach (Li, 2003), and empowered the search for a brain/behavior omnibus.

Furthermore, by using neuropsychological assessment in children to reveal which cognitive processes develop in a consistent manner across cultures, we can compare if these processes are also consistent across cultures in aging individuals at the other end of the life span. Processes that remain consistent across cultures at both ends of the life span would be indicative of a brain/behavior omnibus that is driven from the genome in more of a bottom-up direction. In contrast, an omnibus could be foundational to cognitive ability domains that are consistent across cultures at childhood, but differ more and more across cultures as children mature into adulthood, cognitively adapting across the life span to the ecological necessities of their particular culture in more of a top-down direction. *Using cross-cultural neuropsychology across the life span to evaluate the comparative strength of these two directions in such brain/behavior processes is one of the principal ways that the construct of omnibus adds to the clarification of the mechanisms involved in coconstructivism.*

For example, a comparison of younger and older American and Chinese adults has revealed cultural variation in verbal versus spatial neuropsychological function between the two age groups (Hedden et al., 2002). Visual-spatial measures of working memory and of processing speed was consistent across both cultures in both age groups. However, in the Chinese adults were superior on numerically based working memory and speed of processing. However, this advantage diminished with age and with increasing task demands. Extending such cross-cultural neuropsychological comparisons in verbal and spatial memory to children, would further confirm if visual-spatial working memory reflects a more stable brain/behavior omnibus domain across cultures and across the life span. If so, then the neuropsychological assessment of visual-spatial working memory could enhance understanding of coconstructivism in this specific neuroplastic adaptive domain. It does so by anchoring our attempts to consistently assess the impact of brain injury or enhancement across diverse cultural contexts and at various points across the life span in a multi-dimension manner.

Other examples of the importance of cultural context in cross-cultural neuropsychological assessment

Other neuropsychological measures may not be as useful as omnibus benchmarks for brain/behavior function across cultures and across the life span. For example, processing speed may be a difficult performance measure to apply consistently across cultures. This is because of the comparative value that some cultures place on being slow, thorough, and careful in getting the task correct — as opposed to being fast, efficient, and productive. While it may be a very sensitive performance measure in certain cultural contexts, it may be too sensitive to the motivational context, such as the extent to which a child has learned to value speed in performance over care and accuracy. Such differing motivational value systems for processing speed can, in some cultures, result in processing speed being an insensitive measure to the effects of brain injury or enhanced brain development on overall cognitive ability (Hedden et al., 2002; Jensen and Whang, 1993; Verney et al., 2005).

Likewise, a dynamic approach to assessment for each of these abilities as advocated by Sternberg (2004) and illustrated by Sternberg and Grigorenko (2002) would likely prove even more powerful in evidencing a brain/behavior omnibus through the *cross-cultural neuropsychological study of the plasticity features of injured and non-injured brains across the life span, as they respond to CCRT intervention*. The extent to which the development of cognitive abilities is culture-dependent can only be understood as cross-cultural cognitive assessment takes place with children using a variety of formats (e.g., Helms' interactive "Test Teaching" or Sternberg's Dynamic Assessment format) to evaluate various cognitive ability domains (Helms, 1992; Sternberg and Grigorenko, 2002).

For example, what if cross-cultural neuropsychology with cognitively impaired CM children revealed that targeted rehabilitation interventions for improving attention led to subsequent neuropsychological improvements? Furthermore, what if these improvements occurred not only in static assessment domains as attention, working memory, language function, and reasoning — but also dynamically as a child "learned" to enhance performance in each of these areas? Such findings, if consistently obtained in a variety of cultural settings, would not only help establish the universal nature of such meta-cognitive processes within the omnibus.

We provided evidence for this by using CCRT to improve attention and learning in a consistent manner for both children surviving CM and children with HIV in the Ugandan context. Such interventions have also improved attention and memory in American and Swedish children (Klingberg et al., 2005; Rabiner, 2008). Such cross-cultural neuropsychological evidence in response to CCRT intervention supports the notion of a foundational brain–behavior omnibus amenable to rehabilitative change through positive neuroplasticity. We also presented evidence that cognitive ability is consistently enhanced and diminished by the quality of the developmental milieu for a child in both African and American cultures.

Summarizing how cross-cultural neuropsychology supports coconstructivism as a powerful paradigm in understanding intelligence and culture

The concept of a brain/behavior omnibus is proposed as a way to conceptually interface foundational neuropsychological functions consistent across cultures, with cognitive tendencies and abilities more readily shaped by ecological necessity and cultural experience. We also believe that future cross-cultural neuropsychological research will describe and substantiate the explanatory power of the construct of a universal brain/behavior omnibus.

Once the omnibus has been reasonably characterized in terms of the principal brain/behavior domains, it can then provide a conceptual model for designing and assessing the impact of a given intervention strategy for cognitive or neuropsychological rehabilitation, across cultures (Bangirana et al., 2006). Such measures can also be used to evaluate the extent to which the integrity of the foundational brain/behavior domains is affected in a similar manner across various cultural settings for a given disease. These measures can also be used to see whether a favorable developmental milieu enhances these brain/behavior functions in a consistent manner. If such assessments prove sensitive and specific to the neuropathogenesis of various diseases posing a significant public health threat in these settings, then this provides further evidence for a foundational brain/behavior omnibus.

Furthermore, cross-cultural neuropsychology needs to be applied to children who are at risk from various public health problems that are endemic within the developing world. The brain/behavior development of children over countless generations in the face of infectious diseases commonplace in the tropics (e.g., malaria, meningitis, severe intestinal parasite infections and anemia, schistosomiasis, dengue fever) can provide for a more extensive range of neuropsychological function and corresponding cognitive ability performance within the evolutionary phylogeny dimension of Li's coconstructivist paradigm.

This range of performance in characterizing brain/behavior function is important if one is to use cross-cultural neuropsychology as a platform for better understanding how ecological necessity in differing environments can then shape subsequent cognitive skills and ability profiles. This approach is especially powerful for revealing a foundational brain/behavior omnibus, if neuropsychological cross-cultural evaluations are used not only with developing children, but also in the neuroscience of aging (Park and Gutchess, 2002).

Overview and conclusion

In our review, we have demonstrated that performance patterns in the neuropsychological domains of attention, working memory, and executive reasoning have been consistently demonstrated in several diseases of the brain (CM, SCD, HIV), cultural contexts (i.e., developing world areas, western cultures), quality of developmental milieu, and in response to rehabilitative efforts (i.e., CCRT). Furthermore, these ability domains have been effectively characterized in terms of related brain activation processes through the use of brain imaging technologies in high-income countries. Based on these converging lines of evidence, these ability domains can be considered as reflecting of a foundational brain/behavior omnibus.

Li (2003) has proposed a unified and integrated cross-level dynamic, biocultural coconstructive framework. He contends that such a framework should be able to effectively describe cognitive and behavioral development across the life span. We have reviewed research evidence from cross-cultural neuropsychology in African children. We propose the construct of a foundational brain/behavior omnibus in order to convey how Li's coconstructive framework might be better understood and studied.

As such, it is critical that any neuropsychological assessments applied across cultures be based on the latest cognitive neuroscience and neuroimaging research. This is because the cross-cultural application of neuropsychology assessments has provided a means of methodologically triangulating the omnibus. It does so by using more dynamic assessments across various cultural groups, along with neuroimaging and genomic technologies in both impoverished and resource-rich settings. Cross-cultural neuropsychology, brain imaging, and genomic technologies together can elucidate a brain/behavior omnibus foundational to human plasticity across the life span. The integration of these approaches can provide a powerful new paradigm in understanding the relationship between the developing brain, culture, and cognitive ability. Such a paradigm can help us better understand how, across the life span, ecological necessity sculpts culturally specific cognitive ability profiles; doing so upon a universal brain/behavior omnibus.

Abbreviations

ADHD	attention deficit and hyperactivity disorder
ANCOVA	analysis of covariance
APOE	apolipoprotein epsilon
CC	community control
CCRT	computerized cognitive rehabilitation therapy
CD4	cluster of differentiation 4
CD8	cluster of differentiation 8
CD38	cluster of differentiation 38
CM	cerebral malaria
HIV	human immunodeficiency virus
K-ABC	Kaufman Assessment Battery for Children
K-ABC-2	Kaufman Assessment Battery for Children, 2nd edition

log	natural logarithm
MRI	magnetic resonance imaging
QTL	quantitative trait loci
r	Pearson product–moment correlation coefficient
SCD	sickle-cell disease
SE	standard error
SES	socio-economic status
TNF-alpha	tumor necrotic factor type alpha
TOVA	Test of Variables of Attention
TPT	Tactual Performance Test
UM	uncomplicated malaria
vWF	von Willebrand Factor

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CHAPTER 9

Cultural influences on memory

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Abstract: Research reveals dramatic differences in the ways that people from different cultures perceive the world around them. Individuals from Western cultures tend to focus on that which is object-based, categorically related, or self-relevant whereas people from Eastern cultures tend to focus more on contextual details, similarities, and group-relevant information. These different ways of perceiving the world suggest that culture operates as a lens that directs attention and filters the processing of the environment into memory. The present review describes the behavioral and neural studies exploring the contribution of culture to long-term memory and related processes. By reviewing the extant data on the role of various neural regions in memory and considering unifying frameworks such as a memory specificity approach, we identify some promising directions for future research.

Keywords: culture; cognition; long-term memory; fMRI

Overview

Recent evidence suggests that culture can operate as a lens, bringing distinct aspects of one's environment into focus, based on cultural priorities, values, and experiences. These cultural differences emerge not only in social domains, such as distinguishing the concept of self from other, but also in cognitive domains, such as processing specific aspects of information. Individuals from Western cultures tend to focus on that which is object-based, categorically related, or self-relevant whereas people from Eastern cultures tend to focus more on contextual details, similarities, and group-relevant information. For example, when asked to describe animated vignettes of underwater scenes, Americans' descriptions focus on the prominent fish in the scene, whereas Japanese incorporate many more contextual details, such as the color of the seaweed and water, and the relationship of the fish to the other elements in the scene (Masuda and Nisbett, 2001). These different ways of perceiving the world suggest that culture shapes the ways in which individuals attend to and remember aspects of complex environments.

Over the past few years, studies have begun to explore the contribution of culture to long-term memory (e.g., Chua et al., 2006; Gutchess et al., 2006b; Masuda and Nisbett, 2001; Wang and Conway, 2004; Wang and Ross, 2005), and a few studies have begun to explore the effects of culture on neural processes that contribute to memory (e.g., Goh et al., 2007; Gutchess et al., 2006a; Hedden et al., 2008). This review will first consider the contribution of different neural systems to long-term memory formation and retrieval, and then consider the ways in which culture might modify these processes. Relatively

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few studies address cross-cultural differences in memory, let alone using a neuroscience approach. While we review select findings relevant to the memory literature, we will also discuss promising research directions to investigate the influence of culture on memory systems.

Organization of long-term memory

Core memory system: medial temporal lobes

Since the surgical removal of patient H.M.'s hippocampi, the critical contribution of the hippocampus and medial temporal lobes (MTL) to the formation of new memories has been widely recognized (Scoville and Milner, 1957). In recent years, neuroscience methods have further characterized the role of the MTL and identified the ways in which a number of different processes play into the formation and retrieval of memories. For example, MTL are engaged during the formation of new verbal and visual memories (Brewer et al., 1998; Paller and Wagner, 2002; Wagner et al., 1998). Research with H.M. and other amnesic patients illustrates that remote memories are somewhat accessible even with severe MTL damage (Corkin, 2002), although there is some debate over why this occurs. This finding may reflect the time-limited role for the MTL in retrieval: once information is consolidated to cortical regions, the MTL are no longer necessary for retrieval. Others argue that MTL regions are necessary for retrieving some types of information, such as spatial or autobiographical memories that require vivid reexperiencing of the episode (see review by Moscovitch et al., 2006).

Nevertheless, MTL regions are implicated during some retrieval processes. Some research links discrete retrieval processes to separable anatomical subdivisions of the MTL, with the hippocampus thought to contribute to recollection (vivid reexperiencing of events), parahippocampal cortex implicated in some recollection especially for spatial or non-spatial contexts, and perirhinal cortex responding to familiarity (a more general feeling of prior experience with an event) (Eichenbaum et al., 2007). The MTL also support the retrieval of a complex memory as a seemingly single intact event. In actuality, retrieval relies on the construction of a memory from various features, such as the visual details, sounds, contextual elements, and semantic information about the people and places involved in the event (Schacter et al., 1998, 2007a). These binding processes engage the hippocampus during the retrieval of both veridical accurate memories as well as erroneous false memories (Giovanello et al., 2004; Schacter and Slotnick, 2004).

Contributions of sensory and semantic systems to memory

The involvement of perceptual processes that interpret information from one's environment and individual sensory details underscores the idea that memory is constructive. Encoding visual information engages a host of regions in the occipital cortex, extending into higher-order processing of classes of visual information. Late sensory regions, including the fusiform, lateral occipital complex (LOC), and secondary auditory regions, are implicated in memory for specific classes of features (e.g., Goh et al., 2004; Wheeler et al., 2000). Sensory regions continue to contribute at the time of retrieval, with some evidence suggesting that retrieval relies on the reinstatement of encoding processes. For example, remembering information that had been presented via the auditory or visual modality reengages the same sensory-specific substrates when information is retrieved, even when participants make old/new judgments and do not explicitly recall the perceptual properties of the memories (Wheeler et al., 2000). Recognition of information encountered previously (i.e., true memories) invokes sensory regions of the brain more than false memories (i.e., mistaken beliefs that *new* information was encountered previously) (Schacter and Slotnick, 2004). Likewise, autobiographical memories robustly engage sensory regions, presumably because these personal memories contain rich details and complex visuospatial information (Cabeza and St. Jacques, 2007).

In addition to engaging sensory-specific cortices, encoding and recognition rely on higher-order modules, such as semantic processes. Semantic memory consists of the storehouse of knowledge one acquires over a lifetime about concepts, ideas, and items in the physical world. This knowledge includes information about form, function, and other properties of objects, as well as miscellaneous facts learned or gleaned from experience. As one interacts with the world and forms new memories, experiences integrate knowledge into semantic memory. Naming objects, thinking about object properties such as form and motion, and contemplating actions associated with objects, engage disparate regions of cortex, including lateral temporal, ventral occipitotemporal, inferior frontal, and motor cortices (Martin and Chao, 2001). Autobiographical memory draws on semantic memory, often subserved by middle temporal gyrus (Svoboda et al., 2006). Retrieving stored knowledge about social concepts also relies on temporal regions, specifically anterior regions near the temporal poles (Zahn et al., 2007).

The engagement of sensory regions and many higher-order processes during memory formation and retrieval does not require conscious processing. Priming and other forms of implicit memory, in which prior experience with an item or event facilitates subsequent processing of that information in the future (such as through speeded reaction times), are especially reliant on the physical features of stimuli and corresponding sensory processes (Schacter et al., 2007c). Schacter et al. (2007c) propose a posterior–anterior gradient in the specificity of the neural response to precise sensory details, with posterior perceptual cortices responding precisely to exact repetitions of items (Vuilleumier et al., 2005) whereas later perceptual regions accommodate some variations. More anterior regions, such as lateral temporal and frontal cortices respond on the basis of conceptual information rather than narrow perceptual properties (Schacter et al., 2007c). Posterior neural regions underlying implicit memory typically show an attenuated neural response, or adaptation, when the same item is represented (Grill-Spector et al., 2006). The specificity of the neural response to an item can differ across hemispheres. Whereas the left fusiform adapts to the same *or* different exemplar of an item, the right fusiform response is highly specific, adapting only to the original exemplar (Koutstaal et al., 2001). These distinctions between specific properties of memories apply to both explicit conscious recollection (Garoff-Eaton et al., 2006) as well as implicit measures of unconscious previous experience with an item (Schacter et al., 2004, 2007b, 2009).

Contributions of social, emotional, and reward systems to memory

A number of higher-order processing modalities contribute to memory. The medial prefrontal cortex (mPFC) responds to social information and contributes to memory formation during the successful encoding of social pictures into memory, relative to nonsocial pictures (Harvey et al., 2007). The mPFC is particularly engaged when relating information to the self, over, and above relating information to other people (Craik et al., 1999; Kelley et al., 2002; Macrae et al., 2004), and this extends to autobiographical memory (Cabeza and St. Jacques, 2007). Moreover, mPFC activity during encoding is associated with subsequent recognition of self-referential information, suggesting that the region is implicated not only in thinking about the self, but also plays a critical role in memory (Macrae et al., 2004). Similarly, orienting to social information by forming impressions of individuals engages a dorsal region of mPFC, which is not engaged during a nonsocial comparison task (Mitchell et al., 2004). Interestingly, encoding social information does not reliably engage medial temporal regions in the small number of studies reported thus far. Whether medial prefrontal regions alone are sufficient for encoding, or whether the contributions of the hippocampus and other MTL regions have been obscured through the comparison conditions studied thus far will be resolved through future research.

Social and emotional processes undoubtedly overlap on some dimensions, but Harvey et al. (2007) emphasize the distinct bases for the contribution of these processes to memory. Whereas the amygdala contributes to the encoding of emotional, relative to neutral, pictures, the mPFC responds during the encoding of social information. The role of the amygdala in the encoding and retrieval of emotional information has been established by numerous studies (LaBar and Cabeza, 2006). For emotionally evocative scenes, activation of the amygdala predicts later memory for the scenes (Canli et al., 2000), with evidence that this occurs for negatively and positively valenced information (Hamann et al., 1999). The amygdala also contributes to vivid encoding and retrieval of information, including for autobiographical memory (Cabeza and St. Jacques, 2007). Encoding of visual details engages the amygdala, in concert with fusiform gyrus (Kensinger et al., 2007), and supports "recollection" or "remember" responses, rather than those based on a more general feeling of familiarity (Dolcos et al., 2004; Sharot et al., 2004).

The interface of memory and reward systems has only begun to be explored, but initial findings suggest some intriguing interactions. Activation of reward regions, such as the ventral tegmental area (VTA) and the nucleus accumbens, predicts memory for information associated with high-value rather than low-value rewards (Adcock et al., 2006). Functional connectivity analyses suggest that the VTA, a dopamine-rich midbrain region, works in concert with the hippocampus, indicating a mechanism through which dopamine could modulate memory formation.

Contribution of frontal lobes to memory: modality specificity and control processes

The frontal lobes make myriad contributions to memory processes, consistent with their role in complex cognitive tasks and top–down processing (Miller and Cohen, 2001). Some theories have highlighted hemispheric differences in the frontal lobes' contribution to memory, with distinct modules engaging each hemisphere. Verbal information engages left prefrontal regions whereas visual information engages right prefrontal cortex during encoding (Brewer et al., 1998; Kelley et al., 1998; Kirchhoff et al., 2000; Wagner et al., 1998). Depending on the verbalizability of visual information, such as nameable pictures as opposed to faces, prefrontal cortex may be engaged bilaterally, likely reflecting dual coding of information into both verbal and visual representations (Kelley et al., 1998; Paivio and Csapo, 1973). The material-specific recruitment of prefrontal cortex also occurs during retrieval (Simons and Spiers, 2003). Notably, this hemispheric distinction extends to the MTL (e.g., Kelley et al., 1998).

While ventral regions of lateral prefrontal cortex are sensitive to the modality of materials, the regions contribute to memory through the maintenance and elaboration of information (Simons and Spiers, 2003). In contrast, dorsal prefrontal regions are implicated in controlled processes that draw on working memory and executive functions in order to attend to and select relevant attributes, inhibit distracting information, and maintain goal states (Miller and Cohen, 2001). In terms of memory, these processes aid in the organization and evaluation of information (Simons and Spiers, 2003). The contributions of anterior prefrontal cortex, or frontopolar regions, to memory are less well understood, but some have suggested that the region plays a monitoring function (Buckner and Wheeler, 2001), particularly when information is internally generated (Simons and Spiers, 2003). The distinction between multiple frontally mediated processes is also important in the autobiographical memory literature, with ventral regions engaged during "strategic retrieval, verification, and selection of information from posterior cortical association areas" (p. 2195) and dorsal regions invoked during memory reconstruction, perhaps reflecting the greater monitoring demands for specific personal events (Svoboda et al., 2006). Another distinction in the autobiographical memory literature is between two regions that work together to retrieve detailed personal memories: the lateral prefrontal regions that subserve memory search processes and medial prefrontal regions that underlie self-relevant processes (Cabeza and St. Jacques, 2007).

Several frameworks propose ways in which prefrontal cortex and medial temporal regions interact. Given its role in top–down processing, prefrontal cortex may contribute more in demanding and effortful retrieval contexts when familiarity alone cannot support retrieval (Simons and Spiers, 2003). These situations may include ones in which people must orient attention, remember precise details of a memory (e.g., source details such as recency or perceptual details), create and use elaborated cues, or are under a large memory load. The precise nature of the contribution of prefrontal cortex to memory will depend on the nature of the top–down demands (Simons and Spiers, 2003). According to theories explaining the nature of interactions between the neocortex and hippocampus during memory consolidation, prefrontal cortex could play a larger role in cue generation and memory search over time, as memories are stored cortically and rely less on the hippocampus (McClelland et al., 1995).

While MTL regions interact with a number of distributed regions, to conclude this section we will contrast the nature of the prefrontal–MTL interactions with the interaction of other regions. Whereas prefrontal cortex contributes during effortful and organizational processes that require "working-with-memory" (Moscovitch and Winocur, 1995), other regions respond to the MTL in a more passive manner. Sensory cortices process and share details with MTL regions, and the parietal lobes respond in a receptive manner to the outputs of the MTL. While the parietal lobes have received less attention in the memory literature than other regions, recent evidence suggests that the region responds to familiarity when information is actually old or perceived as such (Wagner et al., 2005). Although some parietal regions track a feeling of remembering, the amount of detail recollected, and whether a person is actively trying to remember information (Wagner et al., 2005), these processes follow from the outputs of memory processes, rather than dynamically guiding what is remembered, as the prefrontal lobes do.

Specificity of memory

A specificity of memory framework considers the ways in which these memory systems can be shaped by culture. This concept captures "the extent to which, and sense in which, an individual's memory is based on retention of specific features of a past experience, or reflects the operation of specialized, highly specific memory processes" (Schacter et al., 2009). A number of behavioral, neuropsychological, and neuroimaging studies reveal a striking specificity to memory processes. For example, true memories (i.e., accurate memory for information encountered previously) contain more sensory information and invoke sensory regions of the brain more than false memories (i.e., mistaken beliefs that new information was encountered previously), whereas imagined information contains information about mental operations and engages corresponding neural regions (Gonsalves and Paller, 2000; Kensinger and Schacter, 2006; Mather et al., 1997; Schacter and Slotnick, 2004). Given the limits on information processing capacity, the specific details encoded and retrieved in memory come at the expense of other details. Comparing the types of details and processes that individuals from one culture prioritize over others offers insight into the type of information given priority in cognition, perhaps reflecting broader cultural values.

The properties of memories and the types of memory errors people commit offer a window into the organization of memory. In terms of types of memory errors, if people falsely remember conceptually related, but not phonologically related items, it suggests that the meaning of the information is critical to the organization of memory, whereas phonological information is not (Chan et al., 2005). Information can be encoded not only in terms of its precise properties (e.g., remembering the unique perceptual features of an item) but also in terms of its gist, or general thematic properties (e.g., a category or verbal label). One example of highly specific memory representation comes from the literature on priming. Priming occurs when prior experience with an item facilitates a response (see review by Schacter et al., 2004). Its effects are implicit: they do not rely on conscious recollection that the item was encountered previously. Although people respond to different exemplars of the same item (e.g., a different picture of a cat) more quickly than to unrelated items, suggesting facilitation from prior exposure to a related item, the benefit is smaller than it is for a repeated presentation of the original item (Koutstaal et al., 2001). This finding indicates that both conceptual and perceptual processes contribute to implicit memory for items. Individuals could differ in the extent to which they emphasize either of these distinct processes. For example, a culture that emphasizes categories and abstraction of information could prioritize conceptual information, which would lead to greater facilitation of related items. In contrast, a culture that is less likely to categorize may process individual items in more detail, thus emphasizing the perceptual aspects and allowing for little benefit for semantically related items.

The concept of memory specificity can also apply to the distinction between unique domains of memory. One example from the social domain is the distinction between self and other: thinking about oneself is vastly different than thinking about other people. The self is associated with memory enhancements, as well as patterns of errors, that do not characterize memories for other people (Rogers et al., 1977, 1979). Neuroimaging methods provide strong support for this distinction by revealing that self-referencing engages a unique region of the brain. Comparison across cultures provides a test of which modules are universals, contributing critically to memory. It is possible that unique memory modules reflect the priority given to particular types of information during processing; the same modules may not exist across all cultures. For example, the emphasis on the ‘‘self’’ as a unique entity may be a larger Western notion (Markus and Kitayama, 1991). If so, self-referencing would not constitute a distinct module in people from all cultures, nor would it disproportionately benefit memory.

In the remainder of this review, we will discuss ways in which culture may shape memory, relating empirical data and new directions to the memory systems explained in the first half of this review. Although investigating the neural underpinnings of cultural differences in memory could provide critical information to localize the stage(s) at which memory process differ, it is also important to consider that content, represented by the qualities and features preserved in memories, may diverge the most across cultures. Relative to differences in cognitive operations, differences in the content of memory may not be as strongly localized to distinct regions, which could make the study of the effects of culture less amenable to neuroscience techniques, or at least reliant on precise experimental manipulations.

Influence of culture on memory: neural and behavioral findings

The above review of the brain regions that contribute to memory formation and retrieval suggests several stages at which culture could shape memory. Cultures could differ in the processing of sensory information or in the top–down control processes that guide what information should be attended to and what should be filtered out. Although none of the studies included in a recent review of the literature on neural differences across cultures directly investigate memory processes, some investigate memory-relevant processes (Han and Northoff, 2008). Those studies suggest that generally cultures differ in intermediate stages of memory processes, such as higher-order visual or semantic processes. Because there are relatively few studies that investigate neural differences across cultures, our discussion of the impact of culture on memory includes behavioral findings and speculation on the neural systems that may contribute to the behavioral differences across cultures.

Cultural differences in MTL systems

As discussed in our review of the role of the MTL in long-term memory, the region is critical to the formation and, in some cases, the retrieval of memories. Given the devastating effects of MTL damage on memory, it seems unlikely that the core memory functions of these regions would differ across cultures; indeed, cultural differences have not been reported in MTL function thus far. However, some of the other ways in which the MTL contribute to memory could be malleable across cultures. For example, recollection and familiarity engage distinct MTL regions; people from different cultures may differ in the types of memory or features of specific memories that are encoded with a rich experience of recollection versus a vague sense of familiarity. This could be particularly true for autobiographical memories, which often consist of vivid contextual detail.

Another way in which MTL function might be expected to differ across cultures is in terms of processing context. Behaviorally, East Asians tend to exhibit a holistic orientation, as a result of the emphasis that Chinese culture places on the collective group and social obligations (Nisbett et al., 2001). In contrast, the emphasis of Greek culture on personal agency contributes to an analytic orientation for Westerners. Studies on cross-cultural differences in orientation to the field/context versus the object converge to suggest that East Asians attend to contextual information, particularly backgrounds in complex scenes, whereas Americans attend to object-based information (e.g., Chua et al., 2005a; Gutchess et al., 2006a, b; Kitayama et al., 2003; Masuda and Nisbett, 2001; Miyamoto et al., 2006; Nisbett and Masuda, 2003). For example, Masuda and Nisbett (2001) reported cultural differences in memory for contextual details, with East Asians recalling more information about background elements of a scene compared to Americans. Although the two cultures did not differ in memory measures for central target objects, East Asians were more impaired than Americans at recognizing the object when the background behind the target object was changed or removed (Masuda and Nisbett, 2001). Based on findings that the parahippocampal gyrus is engaged during the viewing and encoding of complex contexts (Epstein et al., 2001; Epstein and Kanwisher, 1998), East Asians and Americans could be expected to differ in the activation of parahippocampal gyrus. Studies that extended this paradigm, however, did not find differences in MTL function (see Gutchess et al., 2006a, reviewed in next section).

One interpretation of Masuda and Nisbett's (2001) finding is that cultures differ in binding processes, that is, the ability to associate information together into a single representation, such as learning a name-face pairing or the association of an object with a spatial location. Masuda and Nisbett (2001) suggested that Easterners might bind objects to contexts more readily than Westerners, due to cultural differences in the emphasis placed on contexts, particularly social ones. Binding engages the hippocampus during both encoding and retrieval of bound representations (Giovanello et al., 2004; Jackson and Schacter, 2004). Although binding an object to a background engages the hippocampus in young adults (Goh et al., 2004), cultures do not differ in this process (Goh et al., 2007). Behavioral investigations of source memory, the ability to remember which speaker presented particular information, also fails to identify cultural differences across young or older adults in a process thought to rely on associative memory (Chua et al., 2006). Source memory and object-background binding are impaired with aging, likely due to age-related changes in hippocampal function, but these declines are equivalent across American and Chinese cultures (Chua et al., 2006; Goh et al., 2007).

Cultural differences in sensory and semantic systems

Although neuroimaging studies of context memory did not lead to the expected differences in MTL function, research indicates that processing of the component objects differ across cultures. As reviewed in the memory section, sensory-specific regions of cortex respond on the basis of those features, and these same areas may be reactivated at recognition. Thus, we would expect differences in the activation of semantic and sensory regions that correspond to the features and properties that are most highly prioritized, and thus encoded into memory, when the attended qualities differ across cultures.

Evidence exists for cultural differences of this type. In the neuroimaging study to most directly investigate memory, Gutchess et al. (2006a) investigated encoding of complex photographs in East Asian and American participants by comparing pictures of objects alone, pictures of backgrounds alone, and complex pictures containing both objects and meaningfully related backgrounds. Americans engaged object processing regions, including lateral temporal cortex, more than East Asians, but negligible cultural differences emerged in background processing regions (Gutchess et al., 2006a). The authors interpreted the cultural differences in these regions as reflecting semantic processing of objects, consistent with behavioral evidence that Americans may be more object-focused than East Asians. The fMRI data converge with eye-tracking data indicating that Americans make more fixations to objects during the first 300 ms of picture viewing, compared to East Asians (Chua et al., 2005a). Although the cultural differences in the processing of objects reported in Gutchess et al. (2006a) likely impact what information is encoded into memory, it is important to note that these processes may not be specific to memory. Rather, they could reflect broader differences in the processing of objects across cultures. Further investigations targeting selective memory processes, such as successful versus unsuccessful memory formation, would be necessary to evaluate the contribution of these processes to encoding.

Other studies identify cultural differences in perceptual regions. A second study investigating the processing of complex pictures found cultural differences only for older adults (Goh et al., 2007). Whereas young Singaporean and American participants equivalently engaged regions implicated in the processing of picture elements, older adults differed across cultures in the engagement of the LOC, a region associated with visual processing. The LOC responded less for repeated objects in older Singaporeans than Americans, in line with other evidence for selective cultural differences in object processing. An ERP study identified differences in the P1 component, thought to reflect extrastriate activity in response to spatial attention, during a global/local task (Lin et al., 2008). Global processing requires broader attention to larger shapes or portions of space, whereas local processing requiring more focal attention to parts of shapes (e.g., the difference between a large "S" consisting of smaller letter "E"s). This study adopted a different approach to the study of culture; rather than comparing individuals from different cultural groups, the investigators manipulated cultural orientation by priming participants to think more independently or interdependently (i.e., in a relatively more "Western" or "Eastern" style). The result converges with other findings to suggest differences in sensory processes, but the temporal precision afforded by ERP suggests an early locus for cultural differences that could not be identified by previous fMRI studies.

Semantic information is greatly shaped by culture-specific learning and experiences, and the contents of semantic memory differ across cultures (Yoon et al., 2004). The exploration of cross-cultural differences in the organization of information by categories versus similarities or relationships shows that Americans exhibit a preference for sorting by categories whereas East Asians prefer to sort by similarities and relationships (Chiu, 1972; Gutchess et al., 2006b; Ji et al., 2004; Unsworth et al., 2005). These preferences affect effortful cognitive processes as well, with Chinese making more errors than Americans when learning rule-based classification (Norenzayan et al., 2002), and American elderly organizing information in memory by categories more than Chinese elderly (Gutchess et al., 2006b). Based on these behavioral differences, neuroimaging studies would be expected to reveal cultural differences in semantic processing regions, such as temporal and inferior frontal regions. Furthermore, the continual acquisition of semantic knowledge throughout one's life can potentially lead to the magnification of cross-cultural differences over the lifespan, a promising area for future research on universal versus experience-based development of memory (Park and Gutchess, 2006; Park et al., 1999).

Cultural differences in social, emotional, and reward systems

Cultural differences in social processes, particularly in the relationship between the individual and the group, have long been recognized. One useful framework for understanding these differences is the continuum of collectivism–individualism, which suggests that East Asians emphasize relationships and the group, whereas Westerners value uniqueness and independence (Triandis and Suh, 2002). Cultural differences in relationships with others in society impact the concept of the self, with East Asians defining the self in terms of social obligations and networks in an interdependent manner, while Westerners see the self as unique and separate from others in an independent manner (Markus and Kitayama, 1991). Markus and Kitayama (1991) speculated that the "inner self" would be elaborated and accessible for independent individuals, including information about attitudes and desires. This information may be less accessible in memory for interdependent individuals, with information organized in a more context-specific manner (rather than consisting of traits that are generally true across many contexts). This framework is consistent with the finding that after making general judgments about traits, Westerners (or people primed with the concept of the independent self) exhibit better memory for adjectives or other information related to the self whereas East Asians equivalently remember information related to the self or to a close other (Sui et al., 2007; Wagar and Cohen, 2003; Zhu and Zhang, 2002). Recent fMRI work provides converging neuroscience evidence that the relationship between self and others differs across cultures (Zhu et al., 2007). While both Westerners and Chinese differentiate self from distant, unfamiliar others, only Americans differentiate self from close others (i.e., mother) in terms of mPFC activity. Although the fMRI analyses did not explicitly target encoding processes (a post-scan behavioral recognition test confirmed the cultural differences in memory performance), the same region underlies the encoding of self-referenced information into memory (Macrae et al., 2004). This finding suggests that the cultural difference in mPFC likely have implications for memory. The study of bicultural individuals, such as Asian Americans, provides further evidence for the malleability of mPFC activity and self-concept. Priming different aspects of one's self (e.g., with individualistic or collective values) alters orientation to context in making self-reference judgments and corresponding mPFC and posterior cingulate activity (Chiao et al., in press). This finding has implications for the ways in which cultural identity shapes what cues are generated and attended to in order to retrieve information from memory.

Consistent with cultural differences in attention to individuals versus groups and the importance of context, Americans and East Asians differ in their free recall of social interactions. Americans recall more information than Taiwanese participants about the central character relative to other characters, and attribute more intentionality to the characters in their recall of narratives and videos (Chua et al., 2005b). Cultural differences in attention to social contexts also affect judgments of emotion. In their free recall of information, Americans report less emotional content than Taiwanese (Chua et al., 2005b), and conflicting social contexts color the perception of the emotional expression of a target individual for Japanese more than Westerners (Masuda et al., 2008).

Although the neural bases of these cultural influences on emotional memory have not been investigated, other studies identify differences in amygdala activity. Across Japanese and American cultures, the amygdala is more engaged by fearful faces from one's own cultural group, compared to outgroup faces (Chiao et al., 2008). Based on the amygdala's contribution to emotional memory, participants might be expected to form more vivid or detailed memories for ingroup than outgroup fearful faces. Other evidence suggests that cultures differ in their preference for high arousal (e.g., excitement) versus low arousal (e.g., calm) positive emotional states (Tsai et al., 2006). High arousal, rather than valence, particularly drives amygdala activity in American samples (Kensinger and Corkin, 2004); it is possible that the connectivity between the amygdala and the hippocampus or frontal regions differs for East Asians who could prioritize low arousal information more than Americans. Note that it remains to be established whether East Asians' preference for low arousal situations affects information processing.

Some evidence, however, indicates that emotional values influence memory across cultures. When emotional experiences are consistent with values, the information remains in memory longer, thus allowing it to affect other cognitive processes (Oishi et al., 2007). Interestingly, these data indicate cultural differences in the maintenance of information, in contrast to our focus throughout much of this review on the importance of initial attention to information at encoding and the use of appropriate cues during retrieval.

Drawing on both social and emotional processes, the study of autobiographical memory offers a rich avenue to explore how the content of memory differs across collectivist and individualistic cultures. Caucasian Americans tend to recall more individual, as opposed to more social, memories than Asians. In turn, Asians' memories emphasize social interactions and contain more people than do Caucasians' memories (Wang and Conway, 2004; Wang and Ross, 2005). Wang and Ross (2005) suggest that culture affects both initial encoding processes as well as the way in which memory is reconstructed upon retrieval. Cultural differences emerge in early development, with autobiographical memory and self concept reciprocally influencing each other (Wang, 2006). For example, cultural differences in childrearing practices influence the onset of autobiographical memory, with children raised collectively in reformed kibbutzim reporting later first memories than children raised in more individualistic settings (Harpaz-Rotem and Hirst, 2005). These cultural differences in behavioral measures indicate that the types of social, emotional, and perhaps even sensory processes that contribute to autobiographical memory will differ across cultures based on the contents retrieved from autobiographical memory.

Cultural differences in frontally mediated modalities and control systems

The prefrontal cortex plays a multifaceted role in memory, including the maintenance of information and goal states, elaboration of retrieval cues and information to be encoded, and monitoring of internal states and external information from the environment. The demands placed on prefrontal cortex might lead one to suspect that cultural differences would be manifested in a host of frontally mediated memory processes. Surprisingly, only one fMRI study to date strongly implicates prefrontal cortex in cultural differences in cognition. Using a line-judgment task in which judgments could be made in a context-dependent (relative to a frame) or a context-independent (absolute) manner, Hedden et al. (2008) identified a robust fronto-parietal network that was engaged during the effortful judgments. In line with prior work suggesting that East Asians found the absolute judgments more difficult whereas Americans found the relative judgments more challenging, the fronto-parietal network was more engaged during the tasks that participants found difficult, which differed across cultures (Hedden et al., 2008). These results illustrate that tasks can differ in their controlled processing demands in line with cultural priorities and the ease with which strategies can be employed.

The study by Hedden et al. (2008) indicates that strategies that are less practiced within a culture load on similar attentional processes, even though cultures differ in which task is more effortful (i.e., absolute or relative judgments). Other studies indicate that the nature of attention may differ across cultures, with East Asians attending more broadly and Americans attending more focally. These differences allow Americans to respond faster to focal changes, whereas East Asians respond faster to global changes, or to those that are more distributed in space (Boduroglu et al., 2009). In the memory literature, the finding that recent judgments of size affect Japanese participants more than Americans is consistent with the attentional literature in that participants are attending more broadly to recent events still held in memory when making an independent judgment on the current trial (Duffy and Kitayama, 2007). Frontal-parietal networks might be expected to underlie these cultural differences in the breadth of attention.

Investigating cultural differences in prefrontal contributions to autobiographical memory seems promising for future work. The distinctions between regions suggest that ventral and lateral prefrontal activity may be more culture-invariant, as these regions contribute to the effortful processes of search and retrieval (Cabeza and St. Jacques, 2007; Svoboda et al., 2006). Dorsal regions, on the other hand, may be differently engaged across cultures based on which details constitute reconstructed memories and the monitoring demands for those specific details (Svoboda et al., 2006). As reviewed in the previous section, medial regions that reflect self-processing (Cabeza and St. Jacques, 2007) are heavily influenced by culture (Zhu et al., 2007).

Conclusion

While the study of cultural influences in memory is in its infancy, particularly in terms of neural measures, initial studies provide strong evidence that attentional, emotional, and object-based processes differ across cultural groups. A fine line distinguishes the domain of memory from these related processes. For example, memory formation and retrieval depend critically on attention to features of information during encoding and the relevant cues during retrieval. Furthermore, cultural preferences for object versus context, individual versus group-based information, or different emotional states will certainly influence the aspects of experiences that are incorporated into memories, and the component subprocesses used to store and retrieve these memories. A specificity of memory approach draws attention to the different details that are valued and prioritized across cultures, and thus incorporated into memories to varying degrees. Cultural orientations can determine which distinct modules are needed in memory, and whether the organization of memory systems is universal. In this review, we discuss ways in which numerous processes may contribute to cultural differences in long-term memory and how cultural influences may be instantiated neurally, based on our understanding of memory networks in the brain.

We conclude the review by emphasizing the widespread modes of thought and mental states that could exacerbate the influence of culture on the neural underpinnings of long-term memory. For bicultural individuals, testing language influences what information is retrieved from memory (Marian and Kaushanskaya, 2007), a finding that is consistent with effects of language on strategy use and ease of information processing in other domains (e.g., Boroditsky, 2001; Ji et al., 2004). For fluent bilinguals, first and second languages overlap considerably in the brain (Chee et al., 1999); however, language could interact with other processes, such as memory, to magnify cultural differences through its emphasis on different aspects of information and its recruitment of divergent cognitive and social processes. For example, language could alter the lateralization of encoding and retrieval processes, which exhibit a strong left-verbal/right-visual distinction for participants tested in English. Testing in languages that use characters could modify this organizational scheme for memory systems, although this is not the case for linguistic tasks, in which Chinese characters are processed more like English words than pictures (Chee et al., 2000). Even an experience as simple as incidentally viewing pictures of culturally meaningful symbols can lead bicultural individuals to access vastly different knowledge systems. For example, seeing a picture of the Statue of Liberty can lead individuals to make attributions or express a self-concept in line with their independent American identity whereas seeing a picture of the Great Wall of China can induce these same individuals to behave in a manner consistent with their more interdependent Chinese identity (Hong et al., 2000). That such a subtle experience can invoke a dramatic changes in the lens through which one views the world has profound implications for the ways in which information is encoded into and retrieved from memory.

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CHAPTER 10

Numbers in the cultural brain

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Abstract: Recent functional neuroimaging studies have indicated that culture may contribute to differential representation of Arabic numbers in the brain of Chinese and English speakers. The brain networks underlying even very simple arithmetic operation differ among these groups. To what extent do different cultures lead to differences in functional connectivity among the distributed brain areas that constitute the network supporting numerical and arithmetic processes? Key cultural differences are educational system, learning strategy, reading experience, and even genetic background; which ones are important? This review addresses these questions and summarizes findings from recent research on number/arithmetic cognition as well related studies in other cognitive domains. Future directions are also addressed.

Keywords: Arabic numbers; fMRI connectivity; cultural influences

The universal use of Arabic numbers in mathematics raises the question whether they are processed the same way in people of different cultures and languages, such as Chinese and English. To address this question, we used functional magnetic resonance imaging (fMRI) to scan 12 native Chinese speakers (NCS) and 12 native English speakers (NES) with college-level education. The subjects were instructed to perform four tasks during the scanning: (i) *Symbol*: Judgment of the spatial orientation of nonnumerical stimuli in which a triplet of nonsemantic characters or symbols was visually presented either in an upright or in an italic orientation; the task was to decide whether the third symbol had the same orientation as the first two. (ii) *Number*: Judgment of the spatial orientation of numerical stimuli (the task was the same as the *Symbol* condition except for using Arabic digits as visual stimuli). (iii) *Addition*: The numerical addition task was to determine whether the third digit was equal to the sum of the first two in a triplet of Arabic numbers. (iv) *Comparison*: The quantity comparison task was to determine whether the third digit was larger than the larger one of the first two in a triplet of Arabic numbers (see Fig. 1 for examples). A baseline condition of matching white and/or gray circular dots was used to control the motor and nonspecific visual components of the tasks.

Our results indicated a differential cortical representation of numbers between NCS and NES. While the English speakers were found to employ a language process relying on the left perisylvian cortices for mental calculation such as a simple addition task, the Chinese speakers,

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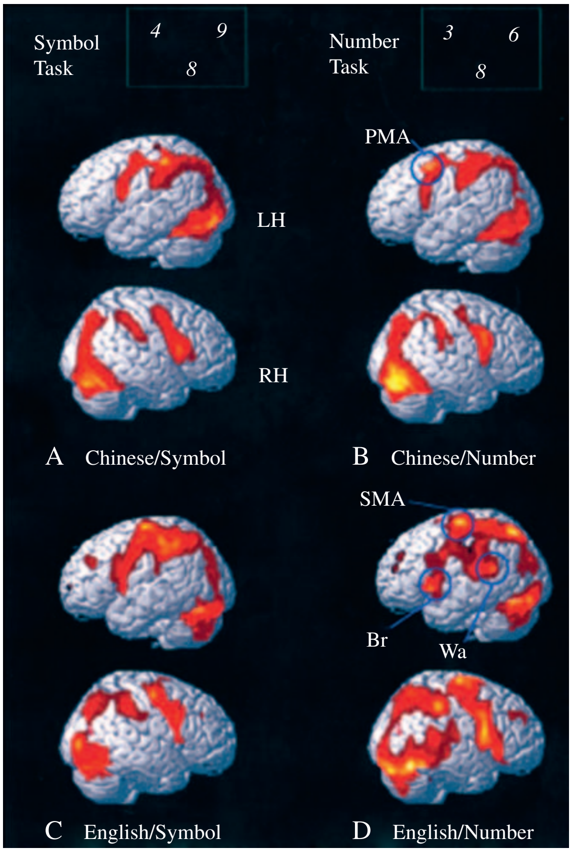


Fig. 1. Dissociation in the brain representation of Arabic numbers between NCS and NES. (A) During the Symbol task in NCS. (B) During the Number task in NCS. (C) During the Symbol task in NES. (D) During the Number task in NES. The task-dependent brain activation was determined by SPM99 by using a liberal threshold ($P < 0.05$) for illustrating a global pattern of the fMRI BOLD signal changes. Type-I error of detecting the differences was corrected for the number of resolution elements at each of the activated brain regions defined anatomically by using the SPM add-on toolbox AAL. The *multiple comparison correction* is the small volume correction (SVC) procedure implemented in SPM. (A and B) Examples of the visual stimuli used for the Symbol and Number tasks, respectively, are shown at the top. LH, left hemisphere; RH, right hemisphere; Br, Broca area.

instead, engaged a visuo-premotor association network for the same task (Tang et al., 2006).

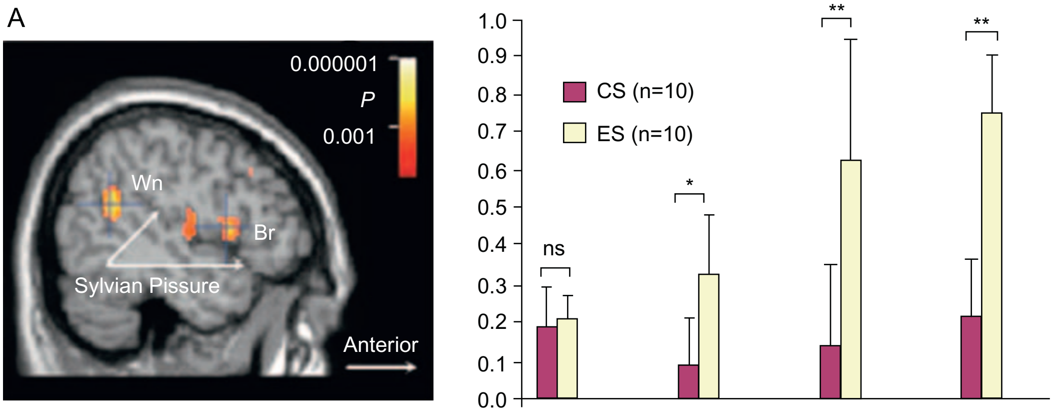
We further chose two regions of interest (ROI) in the perisylvian language region, including both the Broca and Wernicke areas, and in the premotor association area in between BA6, BA8, and BA9 for quantitative analyses by comparing the fMRI signal between the English and Chinese groups. We found the perisylvian activations are significantly larger in the English speakers than in the Chinese speakers (Fig. 2A). As the arithmetic loading increased across all of the four conditions (*Symbol* $<$ *Number* $<$ *Addition* $<$ *Comparison*), there was a trend of increase in the premotor activation in the Chinese speakers but not in the English speakers (Fig. 2B). Therefore, between these two groups, there was a double dissociation in the brain activation during these tasks, supporting clear cultural differences in processing of number.

In both groups the inferior parietal cortex was activated by a task for numerical quantity comparison; however, the ROI-based functional MRI connectivity analyses (He et al., 2003) revealed a distinction between Chinese and English groups among the brain networks involved in the task. In the numerical comparison, two distinct patterns were shown in the functional networks (Fig. 3B and D), in which there was dorsal visuo-pathway dominance (through the parietal–occipital cortex) for the Chinese speakers, but ventral visuo-pathway dominance (through the temporal cortex) for the English speakers.

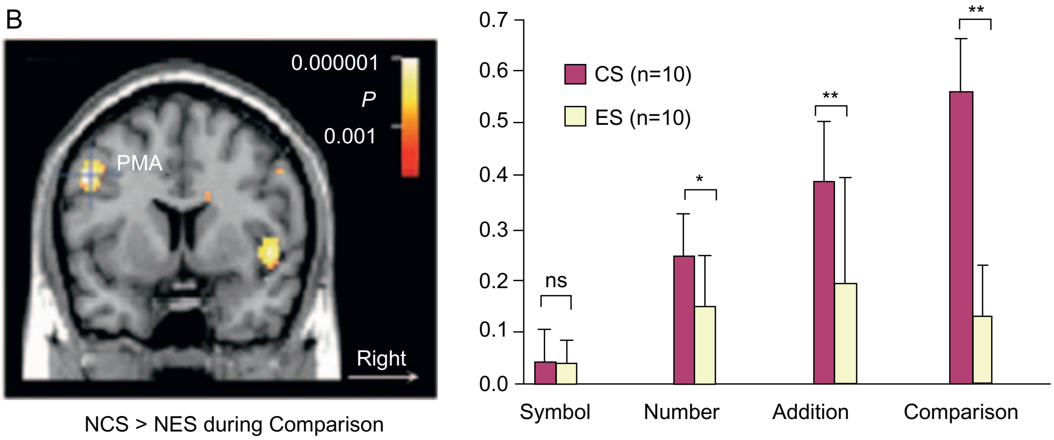
Our findings have two implications. First, in both Chinese and English speakers, there is cortical dissociation between addition and comparison processing. The addition task seems more dependent upon language processing than the comparison task, which is consistent with the suggestion that there are differential neural substrates underlying verbal and numerical processing (Dehaene and Cohen, 1995; Dehaene et al., 1999). Second, there are differences in the brain representation of number processing between Chinese and English speakers. These two different cultural systems may shape the process of Arabic digits differently. These findings might be due to differences between the two cultures in languages, in educational systems, or in genetics. We discuss each of them in the following sections.

Language

Language would be expected to matter more in the addition task than in the comparison task. If so, why during comparison are there much



NES > NCS during Comparison



NCS > NES during Comparison

Fig. 2. Comparison of the activation intensity between NCS and NES in the perisylvian language region (A) and the PMA (B). The brain activation maps (left) were determined by contrasting BOLD signal between NCS and NES only during the Comparison task, with the NES group showing relative increase of the signal (A, English > Chinese) and the NCS group showing relative increase of the signal (B, Chinese > English). The within-group task-dependent activation was determined by SPM99 by using a threshold ($P<0.001$, uncorrected) for defining the ROIs in the perisylvian language region, including both the Broca (Br) and Wernicke (Wn) areas and in the PMA. For each individual, the fMRI activation index (right) was then determined by integrating the BOLD signal changes in these ROIs for statistical comparisons. Two-sample *t*-tests were used to compare the mean of the activation index for each task. *, $P<0.05$; **, $P<0.01$; ns, no significance.

larger differences in the pattern of brain activation between the two groups speaking different languages when the task is less dependent upon language? Several key factors have been considered to contribute to those differences.

First, the brevity of number words in Chinese spoken language allows for faster processing and thus more of them to be represented depending upon short-term memory (Baddeley, 2000; Chein et al., 2002; Ravizza et al., 2004). This might explain the lower activation of perisylvian areas in the Chinese speakers (“I am not sure here what did you mean?”). There is another possibility that the *Comparison* condition with the largest arithmetic load requires most verbal short-term memory which might activate the anterior–posterior brain networks association with the perisylvian areas. This issue, however, should be addressed by further research using the tasks controlling for working memory.

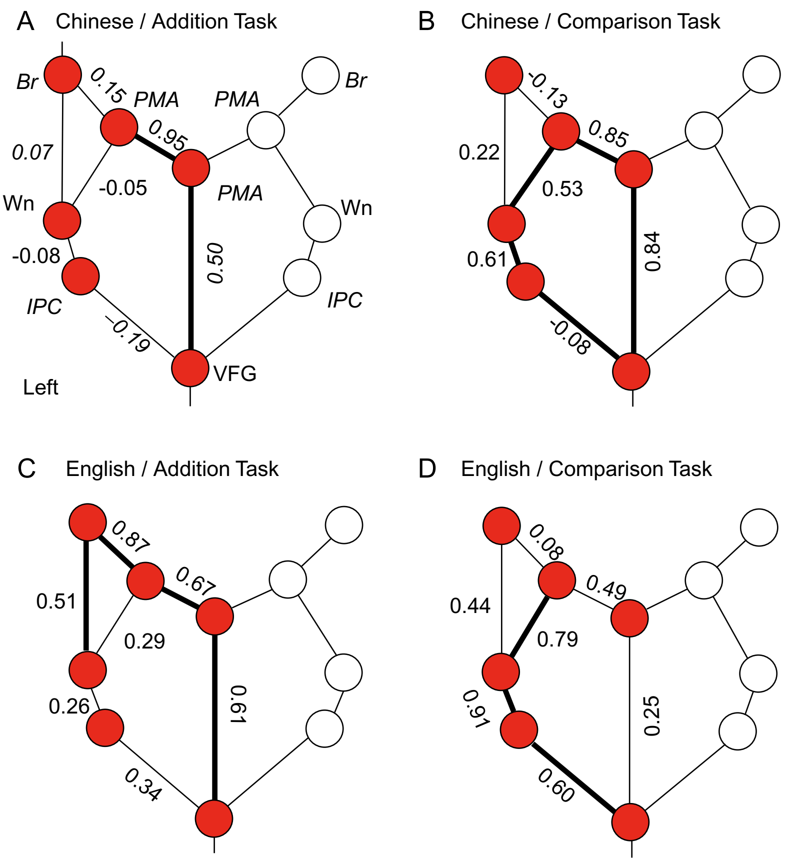


Fig. 3. Differential modulation of arithmetic processing in NCS and NES. The ROI-based functional connectivity analyses show the within-condition interregional covariance of the BOLD signal. (A) During the Addition condition in NCS. (B) During the Comparison condition in NCS. (C) During the Addition condition in NES. (D) During the Comparison condition in NES. The normalized cross-subject covariance $(-1<\mathrm{cc}<1)$ was calculated based on the individual BOLD signal changes in all of the ROIs defined in Figs. 1 and 2. A bold line between two regions (circles) indicates that the region-to-region correlation is statistically significant, reflecting the strength of an effective connection that is modulated by the task. In addition, the networks of the within-condition interregional covariance analysis constructed connections for each condition were statistically different ($P<0.05$) based on comparing one common connection [e.g., Br-Wn for *Addition*; SMA-visual fusiform gyrus (VFG) for *Comparison*] between NES and NCS. For showing the language dependence and for the simplicity, only the Broca area (Br), the PMA, the Wn, the intraparietal cortex (IPC) in the left hemisphere, and the bilateral SMA and VFG were included in the connectivity analysis.

Second, although the language-specific processing may contribute to those differences, the educational systems including learning environment, strategies, and cultural varieties may also have an influence on the acquisition and representation of numerical concepts, and these factors may result in differential brain processes (Posner and Rothbart, 2005; Campbell and Xue, 2001).

Educational systems

Educational systems are different in the East and West, especially in China and the United States (Leung et al., 2006). Campbell and Xue (2001) recruited Canadian university students either of Chinese origin (CC), or non-Asian origin Chinese (NAC) and Chinese university students educated in Asia to solve simple arithmetic problems in four basic operations (e.g., $3+4$, $7-3$, 3×4, $12\div3$) and reported their solution strategies. They also completed a standardized test of more complex multistep arithmetic. For complex arithmetic, Chinese students educated in Asia outperformed both CCs and NACs. For simple arithmetic, however, Chinese educated in Asia and CCs were equal and both performed better than NACs. The authors thought that the superior simple-arithmetic skills of CCs relative to NACs might derive from the extracurricular culture-specific factors rather than differences in formal education. NAC's relatively poor simple-arithmetic performance resulted from both less efficient retrieval skills and greater use of procedural strategies. Nonetheless, all the three groups reported using procedures for the larger simple subtraction and division problems, confirming the importance of procedural knowledge in skilled adults' performance of elementary mathematics. However, there are still other possibilities.

Because of using visual presentation in our previous study, reading experience may have shaped number processing. For example, the strong involvement of visuo-premotor association in the NCS may be related to the experience of reading Chinese logographic characters (Tan et al., 2003, 2006). A Chinese character is composed of strokes and subcharacters that are packed into a square configuration, producing a high, nonlinear visual complexity.

In elementary school, the students learn various strokes and space configurations and memorize the right location of a subunit (from left to right and top to down) for each character. This learning process is carried out by repeatedly copying samples of characters so as to establish the linkage among their orthographic, phonological, and semantic content. Tan et al. (2005) showed that the ability to read Chinese is strongly associated with a child's writing skills and extensive writing exercise during language acquisition. The very different reading experience in Western languages might contribute to the differences in number processing such as greater use of procedural strategies as Campbell and Xue (2001) showed in non-Asian origin Chinese's relatively poor simple-arithmetic performance. Campbell (2008) reported that educated adults often use addition reference to solve large simple subtraction problems, but that they may rely on direct memory retrieval for small subtractions.

Arithmetic strategies

Recent studies investigated the changes in functional neuroanatomy that occur as the Western individuals learn arithmetic problems (Delazer et al., 2003, 2005; Ischebeck et al., 2006). One study compared brain activation during the solving of trained and untrained arithmetic problems. Whereas trained problems showed greater activation of the left angular gyrus, associated with language, untrained problems were found to activate the intraparietal sulcus associated with the number line, suggesting a neural shift from the use of quantitative strategies to verbal retrieval as a function of arithmetic training (Delazer et al., 2003). Delazer et al. (2005) further investigated whether relative shifts in activation differ as a function of particular training methods. Specifically, "training by drill" (rote learning as the result of a two-operant problem) was compared with "training by strategy" (applying an instructed algorithm). Greater activation of the angular gyrus was found during the solving of problems learned by drill than during the solving of those trained using the strategy algorithm. Ischebeck et al. (2006) found that although the angular gyrus was activated more by trained than by untrained multiplication problems, the angular gyrus did not exhibit training effects for subtraction. Thus, the type of instruction and the particular arithmetic operation dynamically modulate the relative activation of intraparietal and left temporoparietal regions during arithmetic processing.

These results are consistent with the notion of ca core system of number, associated with the bilateral intraparietal cortex (IPC) and invariable across cultures, and a distinct perisylvian circuit associated with language- and education-specific strategies for storing and retrieving arithmetic facts (Dehaene and Cohen, 1995).

Genetic and early environmental factors

Representations of numbers occupy reproducible locations within large-scale macromaps, in the bilateral IPC. Dehaene and Cohen (2007) proposed a neuronal recycling hypothesis according to which cultural inventions invade evolutionarily older brain circuits and inherit many of their structural constraints. Since some early brain circuits involving numbers are common to all members of our species, they must be generally shaped by genes. However, genes do differ among individuals and groups. These polymorphisms or alleles are important not only in patients with disorders such as dyslexia and dyscalculia but also among normals. Thus individual differences in the efficiency of numerical networks are likely due in part to these genetic variations. Moreover, it is also known that the expression of genes can be influenced by environmental and training factors producing gene × environment interactions (Green et al., 2008). It is certainly possible that differences in pathways and efficiency in simple mental arithmetic may be due to different allelic patterns in Asian and Western groups. We propose gene–environment interaction framework including genetic factors, educational system, learning strategy, and experience that may contribute to the number processing, see Fig. 4.

Even if genetic variations can account for some of the differences that have been reported, it could still be the case that cultural differences can shape the brain process of number and arithmetic. The major domains of human cultural variability such as arithmetic are tightly constrained by our prior evolution and brain organization as "neuronal recycling hypothesis" proposed (Dehaene and Cohen, 2007). These are the areas where careful research would be needed to establish which genes, if any, are involved in group differences and discover how such genetic variation interacts with training and other cultural influences.

Future directions

Relationship between fronto-parietal networks

Studies suggest the involvement of fronto-parietal networks in the processing of symbolic and nonsymbolic magnitude in humans and nonhuman primates (Ansari et al., 2005; Menon et al., 2000; Nieder et al., 2002; Nieder and Miller, 2004). However, the functional connectivity between prefrontal and parietal activation is still unclear.

New analysis methods such as dynamic causal modeling and Grainger causality modeling of fMRI data may provide insight into network-based representations of numerical magnitude (Ansari, 2008; Friston et al., 2003; Roebroeck et al., 2005).

Interaction between number/arithmetic and language

Reading and arithmetic capacities are developing well into childhood and beyond. How do the differences in number words across languages come to influence the representation and processing of numerical magnitude in the brain? This question should be addressed in the future research.

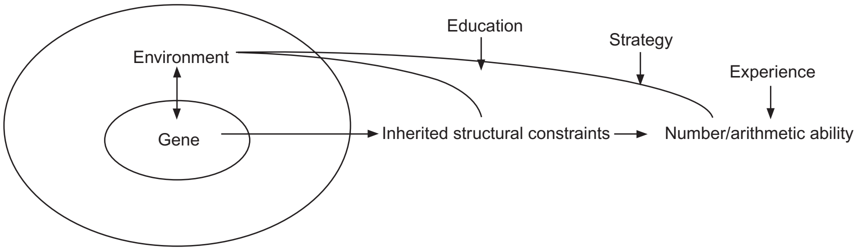


Fig. 4. Gene–environment interaction framework. We propose gene–environment interaction framework including genetic factors, educational system, learning strategy, and experience that may contribute to the number processing.

Gene and environment interaction

If additional evidence suggests that both gene and experience shape human cognitive functions such as number processing in the brain, the next challenge would be to understand how different education systems may change our core intuitions of number differently (Dehaene, 2009).

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CHAPTER 11

Cultural neurolinguistics

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Abstract: As the only species that evolved to possess a language faculty, humans have been surprisingly generative in creating a diverse array of language systems. These systems vary in phonology, morphology, syntax, and written forms. Before the advent of modern brain-imaging techniques, little was known about how differences across languages are reflected in the brain. This chapter aims to provide an overview of an emerging area of research — cultural neurolinguistics — that examines systematic cross-cultural/crosslinguistic variations in the neural networks of languages. We first briefly describe general brain networks for written and spoken languages. We then discuss language-specific brain regions by highlighting differences in neural bases of different scripts (logographic vs. alphabetic scripts), orthographies (transparent vs. nontransparent orthographies), and tonality (tonal vs. atonal languages). We also discuss neural basis of second language and the role of native language experience in second-language acquisition. In the last section, we outline a general model that integrates culture and neural bases of language and discuss future directions of research in this area.

Keywords: cross-cultural; neurolinguistics; language; brain

Ex uno plures (from one, many). Among all the living species, humans are unique in having evolved to possess a universal language faculty and yet speaking more than 6000 different languages. The vast differences across these languages (i.e., phonology, morphology, syntax, semantics, and written forms) both reflect and contribute to historical–cultural differences in human mind (see Sapir, 1921, for a review; Vygotsky, 1986; Whorf, 1956). Because language is such an integral part of culture, anthropologists have relied heavily on language differences (but also on kinship relations, inheritance patterns) to establish cultural groups (Burton et al., 1996). Even the validity of population genetics initially relied on how well their conclusions corresponded to language families (Cavalli-Sforza et al., 1994).

Among the various aspects of culture, language may be the most extensively studied. Language sciences already encompass many disciplines, including the traditional linguistics, anthropology, psychology, information sciences, neuroscience, and their numerous subdisciplines. Researchers in these disciplines, especially in comparative linguistics, have documented differences in the smallest details of the world's languages (see, e.g., Ethnologue: http://www.ethnologue.com/ and the World Atlas of Language Structures: http://wals.info/index). Few other aspects of culture

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have been examined to this extent either qualitatively or quantitatively.

However, these differences, though vast and well documented, have rarely entered the research on neural bases of language. This was perhaps due to two main reasons. First, earlier research on neural bases of language was typically based on patients with brain damages. Their small sample size and great individual variations in the extent and size of injuries or infarctions prevented meaningful comparisons across patients who speak different languages. Second, perhaps more importantly, researchers tended to believe that diversity in languages is purely cultural because infants can learn any language of the world.

Due to the advent of modern brain-imaging techniques, the first obstacle has been overcome. Researchers are able to use fMRI, PET, ERP, and other techniques to study samples of reasonable size from different cultures and to compare their findings with some precision. The second obstacle has been overcome by evidence from decades of research on brain plasticity. Even if the brain is universally the same initially, later experiences (including language experiences) can theoretically lead to diversity at the neural levels (both functionally and anatomically). Chiao and Ambady (2007) have already articulated that culture-specific early experience is one reason that brain structure and function may vary across cultures. After all, the vast differences across languages must be represented somehow at the neuronal level in the brain. The question is whether existing research tools are able to detect them. Indeed, research evidence is accumulating that different languages may have different neural bases. The time may have come for researchers to engage in a systematic exploration of cultural differences in the neural bases of language — cultural neurolinguistics. Specifically, cultural neurolinguistics aims to address questions such as the following. What are the similarities and variations in the brain networks, in terms of both functions and anatomy, that are used to process different languages? How did these variations come about developmentally? What are the implications of these variations for the learning of a new language?

This chapter aims to provide an overview of the emerging literature addressing the above questions. We will first briefly describe the general brain networks for written and spoken languages. Second, we will focus on research on cross-cultural differences in the language networks, emphasizing three distinctions — logographic versus alphabetic languages, transparent versus nontransparent orthographies, and tonal versus atonal languages. Third, we review the literature on the effects of prior language experience on second-language learning. Finally, we will provide an integrative discussion about culture and the neural basis of language and propose some future directions of research in this area.

The language brain

Language is a complex behavior that involves multiple senses and motor skills and the coordination among them. Consequently, the language brain is a network of brain regions that are semi-specialized for different functions. For example, comprehension of spoken language would involve Heschl's gyrus in the primary auditory cortex (bilateral superior temporal gyrus) for initial spectrotemporal and phonological processing, the bilateral posterior inferior and middle temporal gyri for semantic processing, and the left posterior frontal lobe and the temporoparietal area for mapping sounds onto articulatory representations (Hickok and Poeppel, 2004, 2007).

Comprehension of a written language (i.e., reading), on the other hand, would involve the occipital cortex (primary visual analysis), the occipitotemporal regions (visual form processing), the posterior superior temporal gyrus (grapheme-to-phoneme conversion), the superior/middle temporal gyrus (semantic analysis), the inferior frontal gyrus (IFG) (phonological and semantic processing), and the precentral gyrus and cerebellum (motor skills for speech production) (for reviews, see Fiez and Petersen, 1998; Jobard et al., 2003; Paulesu et al., 2000; Price, 1998, 2000). Different types of reading would involve these brain regions to a different extent. For example, according to the dual-route cascade model of reading (Coltheart et al., 2001), there are two routes of phonological access: direct and indirect routes. The direct route (also called the lexical route or the addressed phonology) means that the meaning of a visual word is directly accessed. For the indirect route (also called the sub-lexical route or the assembled phonology), the different phonetic parts of visual words are first processed individually, then assembled (all at the sub-lexical level) to access the sound and the meaning of those words. The IFG appears to be important for both routes of phonological access, although the anterior portion (BA45/47) is more relevant to semantic processing, whereas the posterior portion (BA44/6) is more relevant to phonological processing (Poldrack et al., 1999). Accordingly, it has been proposed that the anterior portion of IFG is more involved in the lexical route, whereas the posterior portion of IFG is more involved in sub-lexical route (Jobard et al., 2003). Furthermore, addressed phonology tends to rely more on the fusiform gyrus in the occipitotemporal region, whereas assembled phonology appears to rely more on the superior temporal gyrus, angular gyrus, and supramarginal gyrus (Fiez and Petersen, 1998; Jobard et al., 2003; Price, 2000). This neural differentiation for different routes of phonological access is important because different languages tend to rely on different routes of phonological access (see next section).

Finally, Indefrey and Levelt (2004) have outlined brain regions involved in speech production: lemma retrieval and selection at the left middle temporal gyrus, phonological code retrieval at the left posterior middle temporal gyrus and posterior superior temporal gyrus, syllabification at the left posterior IFG, articulation at the bilateral sensorimotor and supplementary motor area, and self-monitoring at the bilateral superior temporal gyrus.

Major differences in language systems

Languages differ in many ways, including phonology, morphology, syntax, semantics, and written forms. Based on those differences, linguists have categorized the more than 6000 human languages into major language families (e.g., Niger-Congo, Austronesian, Sino-Tibetan family, Indo-European, and Afro-Asiatic families, with each containing hundreds of languages). Neurolinguistics is at a very early stage in exploring the differences in the neural bases of different languages. In this section, we will focus only on three major differences that have been examined cross-linguistically: scripts, orthography, and tonality.

Scripts

All written languages have their origin in pictographs. Out of those pictographs, some evolved to become logographs such as is the case for Chinese. There is apparent continuity between the visual configurations of the original pictographs and modern Chinese logographs. Modern Chinese logographs, as well as other logographic scripts such as Korean Hangul, typically consist of a number of strokes/units that are packed into a square. In contrast, alphabetic languages such as English use phonetic scripts that are a linear combination of letters (either from the left to the right or from the right to the left as in Hebrew and Arabic, which are also consonants-only scripts called abjads). Sometimes, researchers make a finer distinction between scripts and writing systems. For example, Perfetti et al. (2007) used scripts to describe visual appearance of the characters (logographic vs. alphabetic languages) and used writing system to describe the design principle (i.e., the basic unit size for mapping graphic units onto language units). According to this distinction, Chinese is a morph-syllabic system because Chinese characters map onto meaningful morphemes, whereas English and Korean use the letter-phoneme system, in which characters are mapped onto phonemes in the spoken language.

Orthography

Orthography literally means “correct writing” in Greek. In research literature, it is used to describe how a writing system is implemented in a particular language. Of most relevance to this chapter is the distinction between transparent and nontransparent orthography. Although both

Italian and English use letter-phoneme mapping, Italian has a more regular mapping between letters and phonemes than English. Thus, Italian is a transparent or shallow orthography, whereas English is a quasi-transparent or deep orthography. For transparent orthography, phonological access can be achieved through assembled phonology, in which visual words are transformed into phonology through the grapheme-to-phoneme correspondences (GPC) rules. Korean is also a transparent orthography because of its near-perfect letter-phoneme mapping.

In contrast, Chinese is a nontransparent or the deepest orthography because there is no letter-phoneme mapping in Chinese. For nontransparent orthography, phonological access typically relies on addressed phonology, which directly maps the visual forms of words onto their sounds. For quasi-transparent orthography, such as English, assembled and addressed phonology are used to read regular and irregular words, respectively. It should be pointed out that, with increasing fluency in reading, there is a shift from assembled phonology to addressed phonology.

Due to the absence of GPC rules, Chinese logographic characters are to be learned by drill. Consequently, Chinese children rarely are able to read characters beyond their grade level, whereas many American children can do that because they can rely on the GPC rules (Lee et al., 1995). Consistent with this finding, McBride-Chang et al. (2005) recently found that phonological awareness was more important for reading English than for reading Chinese, whereas morphological structure awareness is more important for reading Chinese than for reading English. For the same reason, dyslexia in English can be of either surface and phonological subtypes (Marshall and Newcombe, 1973), but only of the surface subtype in Chinese (Meng et al., 2005).

Tonality

Pitch in human spoken language can convey several types of information, including speaker's identity, affection, intonation, phonemic stress, and word meaning (Wong et al., 2004; see Wong, 2002, for a review). One typical language-specific pitch is the lexical tone. In tonal languages (e.g., Chinese and Thai), lexical tone is used to distinguish words. For example, in Chinese, the sound /ma/ spoken in a high pitch means "mother," but the same sound spoken in a low falling–rising pitch means "horse." In fact, there are four tones in Chinese Mandarin. The extent of tonality varies greatly across language systems. Languages such as English are atonal and they do not use tones to signal the meanings of words. However, most of atonal languages use stress, which on occasions provides some additional lexical information (e.g., CONtent vs. conTENT).

Different neural networks underlying different languages

The above-mentioned cross-cultural differences in scripts, orthography, and tonality can significantly affect the neural mechanisms of language processing. In a recent meta-analysis of neural bases of reading, Bolger et al. (2005) quantitatively compared the findings of 43 studies of different languages (25 with alphabetic languages, 9 with Chinese, 5 with Japanese Kana, and 4 with Japanese Kanji). They found that activations in the frontotemporal, occipitotemporal, and occipital regions were shared across languages. Important cross-language differences were found in the left middle frontal gyrus (MFG), temporoparietal region, and right fusiform cortex. Gandour (2005) has also provided a summary of the literature on the differential neural networks for tonal and atonal languages. In the following sections, we discuss in detail these relevant findings.

Neural bases of logographic and alphabetic scripts

As mentioned above, the visual configuration varies significantly across different writing systems or scripts. One of such distinctions is between alphabetic and logographic systems. For example, Chinese characters (a typical logographic system) possess a number of intricate strokes that are packed into a square shape, whereas the alphabetic systems have linear combination of letters. Given this visual characteristic of Chinese, the processing of Chinese characters might involve more visuospatial analysis than that of alphabetic writings. Visuospatial analysis (such as whole–part relations) is either bilateral or right-hemisphere dominant (Grill-Spector, 2001; Rossion et al., 2000). Consistent with this view, existing neuroimaging studies on Chinese processing have revealed bilateral or even right-dominated activation in the occipital and posterior occipitotemporal region. For instance, Tan et al. (2000) compared laterality between single Chinese characters and words, and found significant activation in the right occipital cortex for both types of materials. This is in clear contrast with the left-hemisphere dominance in the processing of alphabetic languages (e.g., Price et al., 1996; Vigneau et al., 2005). This finding of greater engagement of the right occipitotemporal region in Chinese processing than alphabetic processing was further confirmed by several other fMRI studies (Bolger et al., 2005; Chen et al., 2002; Fu et al., 2002; Kuo et al., 2001, 2003, 2004; Peng et al., 2003, 2004; Tan et al., 2005; Xue et al., 2005).

Although there is a general consensus that Chinese logographic scripts resulted in the involvement of bilateral primary visual cortex, it is controversial whether the effect of scripts extends upstream to the middle portion of the occipitotemporal area, specifically the fusiform gyrus. Some researchers (Liu et al., 2007; Tan et al., 2000, 2005) have suggested that reading Chinese might be bilateral or even right lateralized in the fusiform gyrus. However, a direct quantitative comparison of the two hemispheres (Xue et al., 2005) revealed left-hemispheric dominance in the fusiform cortex when processing Chinese, a pattern similar to reading alphabetic writings. The latter finding seems to make sense because the fusiform gyrus is believed to play a fundamental role, although not necessarily an exclusive role (see Price and Devlin, 2003, for a review), in processing *abstract* visual word forms (Cohen and Dehaene, 2004; Cohen et al., 2002). Scripts should no longer matter when words are processed at the abstract level. Further complicating the role of the fusiform gyrus in visual word processing and possible cross-cultural differences, other studies have found that this region might also be involved in lexical, multimodal word processing (Buchel et al., 1998; Kronbichler et al., 2004), or in the integration of phonology and visual information during both word and picture processing (McCrory et al., 2005; Price and Friston, 2005; Xue et al., 2006b). Further research can help clarify the role of the fusiform in visual word processing and determine how far upstream scripts can affect the neural basis of language.

Neural bases of transparent and nontransparent orthographies

Depending on orthographic transparency, different languages rely on different routes of phonological access: addressed phonology for nontransparent orthography and assembled phonology for transparent orthography. These different routes of phonological access involve distinct neural mechanisms. Specifically, the left temporoparietal area has been implicated for assembled phonology. In a PET study, Paulesu et al. (2000) found that reading Italian (a transparent orthography) induced more activation in the left posterior superior temporal gyrus than reading English (a quasi-transparent orthography), whereas reading English elicited more activation in the left posterior inferior temporal region and the left IFG. When comparing English with Chinese (a nontransparent orthography), researchers have found that reading English activated the posterior superior temporal gyrus and adjacent supermarginal cortex, whereas reading Chinese activated the dorsal extent of the inferior parietal lobule (perhaps because this area is also involved in visuospatial analysis of Chinese characters) (see Tan et al., 2005, for a review).

There is also evidence that different orthographies might result in differences in other brain regions such as the frontal lobe. For example, Tan and colleagues have found that the left MFG (BA9) is more activated when reading Chinese than when reading English (Tan et al., 2000, 2001, 2005). These researchers believe that this region might play a role in addressed phonology when reading Chinese. They even reported anatomical differences in this region favoring Chinese subjects (Kochunov et al., 2003). Furthermore, they found decreased activation and reduced gray matter in left MFG in Chinese dyslexics (Siok et al., 2004, 2008). However, several other studies have failed to find MFG activation when subjects were reading Chinese (Chee et al., 1999a, 2000, 2003; Kuo et al., 2003; Lee et al., 2004; Xue et al., 2004a, b, 2005; Zhang et al., 2004). It remains to be seen what specific roles this region might play in processing Chinese.

Neural bases of tonal and atonal languages

Previous neuroimaging studies have observed double dissociation in the neural networks of lexical tone and nonlinguistic pitch processing. For lexical tone perception, activations have been mainly reported in the left inferior frontal regions (Gandour et al., 1998, 2000, 2002, 2003; Klein et al., 2001; Wang et al., 2003, 2004) and the temporal regions (Wang et al., 2003, 2007; Xu et al., 2006). In contrast, nonlinguistic pitch processing typically elicit activations in homologous areas in the right hemisphere (e.g., Zatorre et al., 1992, 1994). In speech production, however, Liu et al. (2006) found that tones (suprasegmental elements) activated the right frontal gyrus more than did consonants (segmental elements).

More direct evidence for the effect of linguistic factors or language experience on lexical tone processing comes from crosslinguistic/cross-cultural studies. Recently, several studies have compared neural mechanisms of tone processing in speakers of a tonal language (e.g., Chinese and Thai) with those of an atonal language (e.g., English), and found that speakers of a tonal language showed more left-lateralized activations in the frontotemporal regions in contrast with atonal language speakers (Gandour et al., 2003, 1998; Klein et al., 2001; Wong et al., 2004; Xu et al., 2006). There is evidence that the left hemisphere is more effective in learning lexical tones than the right hemisphere (Wong et al., 2007).

Furthermore, tone processing appears to be language specific. Neural patterns of tone processing do not seem to transfer from one tonal language to another tonal language. For example, when processing Thai tones, native Chinese speakers, although having years of experience in Chinese tones, showed different neural patterns from those of native Thai speakers (Gandour et al., 2002, 2003).

Other cross-cultural differences in the neural basis of language processing

Although cross-cultural differences in neural bases of speech processing and reading have been most often studied, researchers have also begun to document cross-cultural differences in neural bases of other aspects of language processing. For example, studies of speakers of English and other Indo-European languages have typically found that verbs are represented in the frontal region (e.g., the left prefrontal cortex), whereas nouns are represented in the posterior regions (the temporal–occipital regions) (Petersen et al., 1989). Nouns and verbs in Chinese, however, activate a wide range of overlapping brain areas in distributed networks, in both the left and the right hemispheres (Li et al., 2004). The reason for this cross-cultural difference is probably that categorization of words into different grammatical classes is less clear-cut in Chinese than in English. Many individual words in Chinese cannot be easily distinguished into nouns or verbs, mainly due to a lack of inflectional morphology in Chinese. Most words play multiple grammatical roles, resulting in an abundance of class-ambiguous words that can be used as either nouns or verbs. Much more research is needed to understand crosslinguistic variations in the neural bases of semantic processing.

Second-language learning

Thus far, we have focused on comparisons of neural bases of different languages. Cultures are not isolated from one another. Cultural encounters lead to exposure to and acquisition of second languages. Neural bases of second language, especially the role of native language in second-language acquisition, are an important topic of research in cultural neurolinguistics.

Earlier studies of bilinguals (Dehaene et al., 1997; Kim et al., 1997; Perani et al., 1998) reported neural dissociations between native and second language. Later studies typically found a largely shared neural network in both native and second-language processing, even for two drastically different languages such as Chinese and English (Chee et al., 1999a, b, 2000; Klein, 2003; Klein et al., 1995, 1999; Xue et al., 2004a, b). Given the differences in neural networks for different native languages (see the previous section), it is puzzling why neural patterns for first and second language (especially for Chinese and English) are not more distinct. One explanation of this overlap between native and second language's neural networks is that the neural mechanisms for second-language processing are shaped by native language experience. In fact, some recent studies showed that the brain network shaped by native language experience is optimal for learning a new language (Chen et al., 2007; Dong et al., 2008; Mei et al., 2008; Xue et al., 2006a).

Perfetti et al. (2007) have proposed an intriguing model that consists of two processes, namely assimilation and accommodation in Piagetian sense, to account for the effects of the native language on neural mechanisms involved in learning a second language. The assimilation hypothesis assumes that the brain will read a second language as if it is the native language and use the native language network to support the second language. In contrast, the accommodation hypothesis assumes that the brain's reading network must adapt to the features of a new writing system to the extent that those features require different reading procedures. Supporting evidence for this model comes from several studies. For example, a study by Tan et al. (2003) provided evidence for neural assimilation by showing that for Chinese subjects who were learning English as their second language, the superior temporal gyrus was not activated when reading English although this region was activated for native English readers. Instead, the left MFG, usually involved in processing Chinese, was activated. On the other hand, for English speakers who are learning Chinese, the bilateral visual form and left MFG were activated when processing Chinese, which is consistent with the accommodation hypothesis (Liu et al., 2007; Nelson et al., 2009). Taken together these studies, one might conclude that Chinese speakers are more likely to assimilate, but English speakers are more likely to accommodate. Of course, it is also likely that, given the differences in linguistic features, non-transparent logographic language demands accommodation, whereas transparent alphabetic language allows for accommodation. These possibilities need to be tested with a design involving native speakers of two different languages learning the *same* second language. So far, no imaging study of such a design has been conducted.

Integrating culture into neurolinguistics

As mentioned earlier, cultural neurolinguistics is only at the beginning stage of development. Thus far, most research has focused only on the effects of language features on the brain. Much is to be done regarding other aspects of culture's impact on the language brain. In this section, we outline a sketch of this emerging field (see Fig. 1). This field needs to address both classic and new questions such as how the interaction between the features of languages and the brain anatomy and function affect the neural basis of different languages, how first- and second-language acquisition can affect the brain (accommodation), how brain development shapes the neural mechanisms for first- and second-language acquisition and development (assimilation), how social factors (e.g., social economical status, education, vocabulary and knowledge explosion, technology use, communication style, cultural orientation, etc.) that shape the language use and experiences would shape the brain (e.g., Raizada et al., 2008), and finally how language and the brain coevolve to create the diversity in languages and the diversity in neural bases of languages.

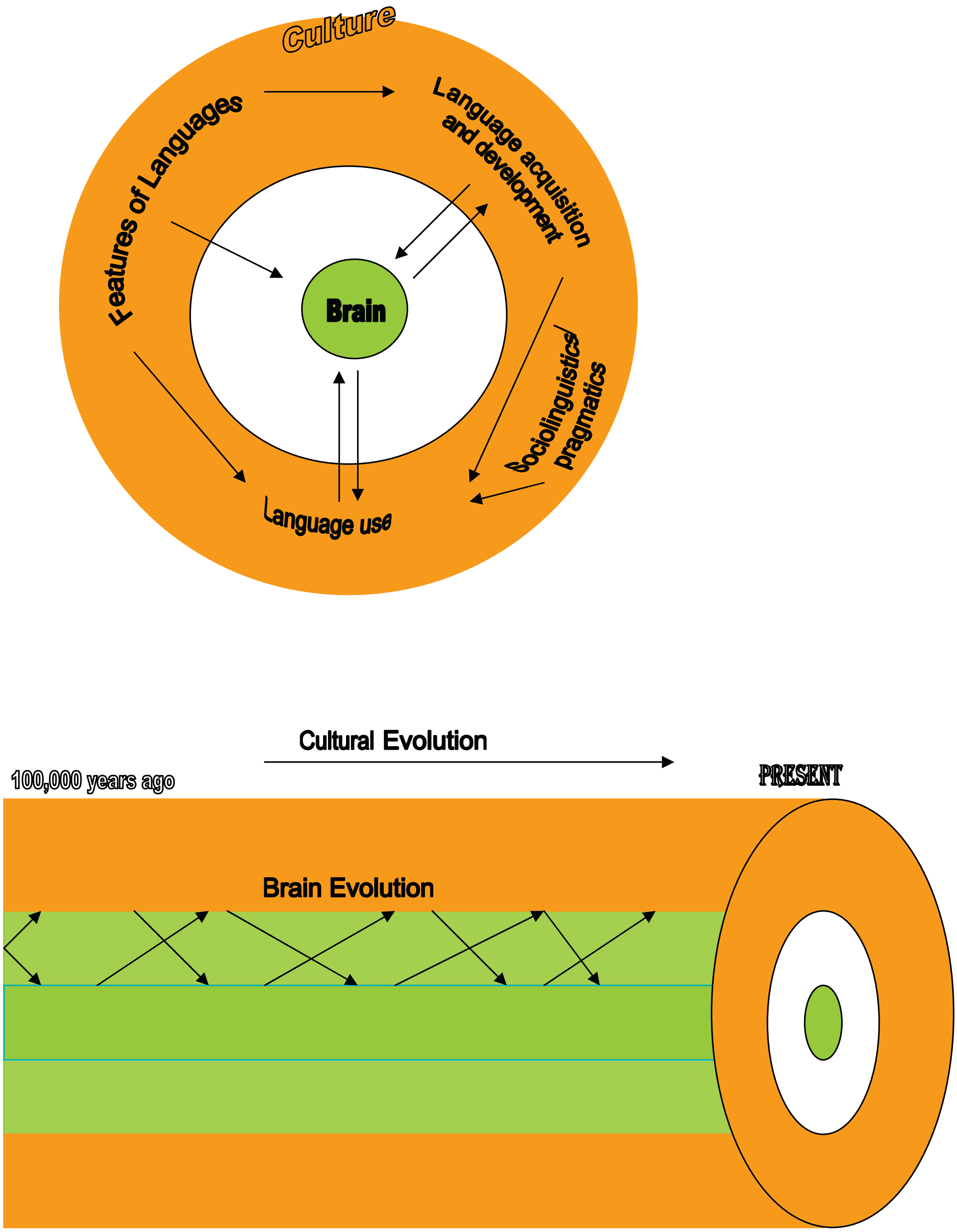

Fig. 1. A schematic presentation of the interrelations among culture, language, and the brain.

The last two areas are almost virgin territories. Language is not content free, so sociolinguistic factors (e.g., communication style), sociopsychological factors (e.g., self descriptions, interpersonal relations), or the use of language in other cognitive tasks (such as arithmetic) can all affect brain mechanisms. A few groups of researchers have already begun to document the effects of larger cultural contexts on brain functions. For example, Han and Northoff (2008) recently reviewed several studies showing the effect of culture on the social brain. Tang et al. (2006) showed cultural effects on the mathematical brain. Similarly, Zhou et al. (2007a, b) have systematically demonstrated that different cultures' approach to teaching mathematics can affect the brain bases of mathematical learning. Given that language is the medium (or "tool") of cultural representations (Vygotsky, 1986), future research needs to systematically examine how language mediates these cross-cultural differences in brain functions.

More theoretical and empirical work is also needed to delineate the mechanisms involved in the bidirectional effects between culture/language and the brain. Some theoretical discussions have already started. For example, Fabrega (1977, 1982) has suggested three distinct ways, occurring at different stage of development, in which cultural factors might help mold the human brain. First, the ecological surroundings associated with a certain culture may selectively activate or "tune" appropriate neuronal connections. Second, cultural factors in early child learning differentially and dynamically alter brain development. Finally, life-long adaptability allows the adult brain to continuously adapt to new situations. Dehaene and Cohen (2007) recently presented a cultural recycling model, which suggests that preexisting brain circuitry places structural constraints on the brain-cognition mapping (e.g., visual words mapping onto the left fusiform gyrus across cultures), but brain plasticity allows flexibility in the specifics of the mapping.

Common across these and other models (such as Perfetti's accommodation and assimilation model) are their emphasis on two neurobiological principles: neural plasticity and specialization. Neural plasticity allows culture to have an imprint on the brain, and neural specialization sustains cross-cultural differences in the brain. As presented earlier, language features (e.g., scripts, orthographies, and tonality) can determine the neural bases of language learning through neural specialization. Furthermore, these neural bases may carry over to second-language learning (Nakada et al., 2001; Tan et al., 2003). In a way, this discussion of neural specialization in general language learning is just an extension of the classic example of neural specialization in phonetic processing. At birth, infants are universally capable of differentiating phonetic contrasts in all languages. As a result of native language experience (or "tuning"), however, the ability to distinguish nonnative phonetic contrasts dramatically declines as early as 6 months (Kuhl and Rivera-Gaxiola, 2008; Kuhl et al., 2006; Werker and Tees, 1992). By 11 months of age, Japanese infants can no longer distinguish /ra/ from /la/, and American infants cannot distinguish Chinese sounds /chi/ and /ci/ (Kuhl et al., 2001). English speakers cannot identify Hindi phonetic contrasts that differ in voice onset time from −90 to 0 ms (Sharma and Dorman, 2000). When these speakers learn a new language, they will have "accents" (i.e., assimilation). For more discussions about this topic, readers can refer to Perceptual Assimilation Model (Best et al., 2001) and Natural Language Magnet model (Iverson and Kuhl, 1996).

In tandem with neural specialization is neural plasticity, which makes accommodation possible. For example, even though infants begin to lose sensitivity to nonnative phonemes, they can learn a new language without accents until about 10–12 years of age. Neural plasticity is at work here and it allows the brain to accommodate to foreign sounds. In fact, evidence is accumulating that language learning can change brain functions and even anatomy due to neural plasticity. For example, phonetic training can induce functional reorganization such as an expansion of existing regions and the recruitment of additional regions (Callan et al., 2003; Wang et al., 2003). Auditory training can ameliorate the dysfunction of the inferior frontal and temporoparietal regions in dyslexia (Temple et al., 2003). Braille readers who became blind early in life were found to rewire their visual cortex to respond to tactile tasks (Sadato et al., 1996). Finally, language learning can also result in permanent changes in brain structure. Bilinguals have been found to show increased gray matter density in the left inferior parietal region as compared to monolinguals (Mechelli et al., 2004). This study further revealed that the gray matter density was positively correlated with second-language proficiency and negatively correlated with age at acquisition of second language, suggesting that more learning resulted in greater structural changes in the brain.

This dynamic process of accommodation and assimilation or plasticity and specialization is likely to occur across all aspects of culture–brain connections, and across the life span. So far researchers have only uncovered a limited number of instances such as phonetic processing and visual words processing (see an earlier section). All other links in our general model (see Fig. 1) can be examined from this dynamic perspective. Beyond the links in the model, an optimistic view is that the near future will also witness the integration of culture into neurosciences at even a broader level, including molecular genetics (see Chiao and Ambady, 2007).

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SECTION IV

Cultural Neuroscience of Social Cognition

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CHAPTER 12

Culture in the mind's mirror: how anthropology and neuroscience can inform a model of the neural substrate for cultural imitative learning

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Abstract: Cultural neuroscience, the study of how cultural experience shapes the brain, is an emerging subdiscipline in the neurosciences. Yet, a foundational question to the study of culture and the brain remains neglected by neuroscientific inquiry: "How does cultural information get into the brain in the first place?" Fortunately, the tools needed to explore the neural architecture of cultural learning — anthropological theories and cognitive neuroscience methodologies — already exist; they are merely separated by disciplinary boundaries. Here we review anthropological theories of cultural learning derived from fieldwork and modeling; since cultural learning theory suggests that sophisticated imitation abilities are at the core of human cultural learning, we focus our review on cultural imitative learning. Accordingly we proceed to discuss the neural underpinnings of imitation and other mechanisms important for cultural learning: learning biases, mental state attribution, and reinforcement learning. Using cultural neuroscience theory and cognitive neuroscience research as our guides, we then propose a preliminary model of the neural architecture of cultural learning. Finally, we discuss future studies needed to test this model and fully explore and explain the neural underpinnings of cultural imitative learning.

Keywords: cultural learning; imitative learning; imitation; neuroimaging; mirror neuron system; cultural neuroscience

Introduction

The emerging subfield of cultural neuroscience is based on the concept that cultural experience shapes the human brain, an idea that is increasingly accepted and studied in neuroscience. Yet a more basic question remains unaddressed in the realm of neuroscience: "How did the cultural information get into the brain in the first place?" In this paper we review literature from both anthropology and cognitive neuroscience that may help to elucidate the neural architecture of enculturation.

Before we can design effective studies to investigate how differential cultural experience shapes the human brain, we must have a better

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understanding of the neurocognitive mechanisms of cultural learning. Fortunately, the conceptual and methodological tools needed to conduct effective neuroscientific investigations of cultural learning already exist; anthropology provides a number of complementary theories of cultural learning, while cognitive neuroscience provides the methods and technologies needed to discover the neural architecture that likely underlies cultural learning. Boundaries between these disciplines, however, have until recently prevented their union.

Anthropological theories of cultural learning are based on fieldwork, computational modeling, and laboratory experiments. These theories converge on several cognitive mechanisms suggested to be fundamental to human cultural learning. The prevailing view is that the core of human cultural learning is sophisticated imitative learning (Higgs, 2000; Hurley and Chater, 2005; Kannetzky, 2007; Meltzoff and Prinz, 2002; Sommerville and Decety, 2006; Tomasello et al., 1993b) which is augmented by forms of learning biases (Henrich and McElreath, 2003), mental state attribution (Tomasello et al., 1993a), and reinforcement learning (Castro and Toro, 2004).

Fortunately, cognitive neuroscience studies have already provided us a great deal of knowledge about the neural architecture of imitation, learning biases, mental state attribution, and reinforcement learning in vivo through the use of neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). Thus, by using anthropological cultural learning theory to guide future neuroimaging investigations of imitation, we can better understand the neurocognitive architecture of cultural learning. This can, in turn, inform our study of how differing cultural experience shapes other neurocognitive systems and of the neurocognitive machinery of cultural learning itself.

This review is organized into three sections. The first section treats theoretical and behavioral accounts of cultural learning, with a focus on imitative learning. The second section describes neural systems that may underlie the cognitive components of cultural imitative learning. In the third section, we propose a preliminary model of the neural architecture of cultural imitative learning and suggest future studies needed to test this model.

Section I: cultural learning and imitation — theory and behavior

Cultural learning

In the following discussion of cultural learning theory we will briefly define cultural learning and highlight aspects of human cultural learning that differ from the cultural capacities of other animals. We utilize this comparative perspective to focus our discussion of cultural learning on aspects of human cognition that may be most informative for elucidating the neural underpinnings of the sophistication of human cultural capacities.

The first step in discussing cultural learning is defining culture itself. Bates and Plog (1990, p. 7) define culture as "the system of shared beliefs, values, customs, behaviours, and artifacts that the members of society use to cope with their world and with one another, and that are transmitted from generation to generation through learning". This definition highlights a critical point: culture is not merely the sum of cultural products: beliefs, behaviors, and artifacts; instead culture is created through the transmission and modification of these products within and between generations: cultural learning. Thus, by studying cultural learning and its neural basis, we will not only be studying the way in which culture is transmitted, we will also be studying a critical component of culture itself.

Tomasello et al. (1993a) describe cultural learning as a form of social learning in which perspective-taking plays a critical role in both the transmission of information and the resulting cognitive product. In other words, during cultural learning, information in addition to modeled behaviors, such as the inferred intentions and emotional states of the model, are encoded and retained along with the behavior in order to give that behavior contextual meaning. Tomasello et al. (1993a) propose that cultural learning includes imitative learning, instructed learning, and collaborative learning — these types of learning emerge in successive stages of development. Cultural learning is distinguished from other forms of learning by its social nature and the niche it occupies within the learning environment. Modeling work by McElreath (2004) demonstrates that cultural learning is favored when individual learning is costly and inaccurate. Boyd and Richerson (1985) suggest that human social learning abilities were evolutionarily favored as a strategy for learning information relevant to rapidly changing environmental conditions.

Culture and cultural transmission are most fully developed in humans; however, great apes, especially chimpanzees, also have basic cultural capacities. A number of studies in both captive and wild chimpanzees have documented rich behavioral traditions specific to particular groups (Boesch, 2003; McGrew, 1992; Wrangham et al., 1994). Additionally, several recent experimental studies in groups of captive chimpanzees have demonstrated faithful transmission of food retrieval techniques (Whiten et al., 2007), as well as arbitrary actions (Bonnie et al., 2007) taught to a few group members throughout the group and, in the case of Whiten et al. (2007), between groups that had only visual contact. These experiments demonstrate with a new level of empirical certainty that chimpanzee groups can not only maintain unique cultural repertories, but also that — as in humans — a prominent means of chimpanzee cultural transmission is imitative learning.

The notion of chimpanzee culture and chimpanzee imitative cultural learning raises the question, "What explains the formidable differences between human and chimpanzee culture?" The answers may lie in the accuracy and complexity of human imitation abilities, compared to those of chimpanzees, and in the other cognitive mechanisms that augment human imitation, such as learning biases, mental state attribution, and reinforcement learning. The unique combination, and degree of sophistication, of these cognitive abilities enable humans to encode inferred intentions, emotions, and reward values along with learned behaviors. This contextual information allows individuals to modify culturally learned behaviors. In turn, the continual modification of culturally learned behavior leads to the summing of cognitive resources within and between generations and the creation of distinct and rich cultures that are constantly evolving (Henrich and McElreath, 2003; Tomasello, 1999; Tomasello et al., 1993a). We will structure our discussion of cultural learning around the suite of cognitive mechanisms that distinguish human from nonhuman cultural capacities as the neural underpinnings of these abilities may be most informative in revealing the neural architecture of human cultural learning.

Imitation and imitative learning

Imitation learning is at the core of cultural learning; therefore, cultural imitative learning will be the focus of our review. In the following section we will provide a broad overview of imitative learning including its definition, theoretical accounts of the mechanisms of imitation, and behavioral accounts of imitation learning at different stages of development.

Although the meaning of the word "imitation" seems intuitive, the precise definition of imitation and imitative learning has been the subject of much debate (Chalmeau and Gallo, 1993). The imitation controversy is due in part to the question of whether there are any uniquely human abilities (Miklósi, 1999). Additionally, there are a number of mimetic but nonimitative processes, such as contagion and observational conditioning, that can result in the appearance or behavior of one individual resembling that of another (Zentall, 2006). Two mimetic processes closely related to but distinct from imitation are stimulus enhancement, in which an individual's attention is drawn toward a particular *object*, and goal emulation, where an individual learns the *goal* of an action but may accomplish that goal by other means (Whiten, 2000). True imitation is distinguished by the faithful copying of the *means* by which a goal is achieved (Whiten, 2000; Zentall, 2006). Tomasello et al. (1993a) argues that true imitation requires recognizing the intentional structure of the modeled behavior. Intention recognition is especially important during a special type of imitation termed opaque imitation (Piaget, 1962) [also called blind or cross-modal imitation (Moore, 2004)], which involves imitation with a body part to which the imitator does not have direct visual access, such as the face.

There is also some debate over the neurocognitive mechanism of imitation. Iacoboni (2009) states that the two psychological theories of imitation mechanisms that best fit neurophysiological data are the ideomotor framework and the associated sequence-learning model. The ideomotor framework postulates that imitation is achieved through a shared neural representation system for observation and execution (Prinz, 2005). In the associative sequence-learning model, rather than a single neural substrate linking observation and execution, experience-based Hebbian learning (the strengthening of neural connections due to repeated coincident neural firing) links separate neural systems for observation and execution (Heyes, 2005).

In addition to theoretical accounts of the mechanisms of imitative behavior, extensive behavioral studies of imitation have been conducted from the neonatal period through adulthood. There is considerable evidence that the basic neurocognitive machinery of imitation is hardwired. For example, Meltzoff and Moore (1977, 1983, 1989) found imitation of facial and manual gestures such as protruding the tongue in infants only hours old; this finding has since been replicated in 13 independent laboratories (Meltzoff and Decety, 2003). In addition to innate imitation mechanisms, which results in the basic forms of imitation seen in infants, elements of the human socio-cultural environment, such as joint attention and turn-taking, promote the rapid development of more sophisticated imitative abilities (Kumashiro et al., 2003). The imitation-promoting effects of the human socio-cultural environment are strikingly illustrated by Tomasello et al.'s (1993b) finding that children and enculturated chimpanzees perform similarly on an imitation task and outperform non-enculturated chimpanzees.

Human imitative abilities reach a high level very early in life. Infants as young as 12 months are sensitive to the rationality of modeled actions (Schwier et al., 2006), and at 18 months, they have been found to imitate object-directed real and pretend actions (Rakoczy et al., 2005), as well as imitate the goal of incomplete actions (Meltzoff, 1995). Because of the early emergence of imitative abilities, imitation makes up a large portion of social interaction during early development (Masur, 2006) and is the likely means by which many important types of cultural information, such as language and behavioral norms, are learned (Arbib, 2005).

An ongoing debate is whether the motor system is engaged during action observation, as suggested by the ideomotor framework, or whether connections between observation and action only happen during reenactment of the behavior (Iacoboni, 2009; Vogt and Thomaschke, 2007). A number of studies suggest that, in the domains of imitative learning of sequences, timing, and task dynamics, pure observation has an equivalent effect to motor practice on later behavioral performance. However, for configural postures and inter-limb coordination the data are less clear and motor practice may result in superior behavioral performance (for a review see Vogt and Thomaschke, 2007). It is important to note that even in cases when observational and motor practice appear equivalent, nether strategy results in a carbon copy of the imitated action. Rather, observational practice results in elements of the imitator's own behavioral repertoire being activated and built upon (Greer et al., 2006; Iacoboni, 2009; Vogt and Thomaschke, 2007).

Reinforcement is another critical element of imitation learning as it guides both the likelihood and direction of learning. Both internal and external reinforcement of the imitator influence the likelihood and direction of imitative learning (Greer et al., 2006). Reward and punishment of the model (vicarious reinforcement) has also been found to influence imitation (Bandura, 1971). Finally, motivation at the time of observation (e.g., whether the imitator is hungry or sated while observing a food retrieval task) can also affect the probability of later imitation (Dorrance and Zentall, 2001).

Greer et al. (2006) distinguished between performance of modeled behaviors already in the imitator's repertoire and imitative learning of novel behaviors. In particular, they suggest that learning of novel behaviors and performance of previously learned behaviors can be differentially affected by reinforcement. An imitation learning study by Bandura (1965) illustrates these differential effects of reward on learning and performance. Bandura showed subjects modeled behavior that was either vicariously rewarded or punished. Following behavioral modeling, subjects were directly provided incentives for imitation. These incentives resulted in the production of learned but previously unimitated behaviors, suggesting that vicarious reinforcement influenced the imitation but not the learning of modeled behaviors (Bandura, 1965).

In summary, imitative learning consists of many components including imitation of timing, configural postures, sequences, and reinforcement sensitivity. Action observation likely activates the motor system, which facilitates imitative learning. Sophisticated imitation abilities are clearly key to human cultural learning especially early in life, but they are likely not the whole story. Comparative studies of primate cognition, modeling studies, and human ethnographic work have identified several other cognitive mechanisms that augment our imitative abilities during cultural learning and have likely been instrumental in the dramatic explosion of cultural capacities in *Homo sapiens*. In the following section we will discuss three of these hallmarks of human cultural learning: learning biases, mental state attribution, and flexible reinforcement learning.

Learning biases

Cultural learning is not indiscriminate; rather it is biased toward certain contexts and content, which likely results in the more efficient acquisition of knowledge, beliefs, and practices (Henrich and McElreath, 2003). Context biases result in the information held by certain individuals (model-based bias) or the highest frequency information (frequency-based bias) being favored (Henrich and McElreath, 2003). Henrich and Boyd (1998) argue that the cognitive mechanisms supporting these learning biases were likely shaped by natural selection.

A number of empirical laboratory studies conducted by Bandura and his colleagues (Bandura et al., 1961, 1963) suggest that high model-observer similarity favorably biases social learning. Based on these studies, Bandura proposed his Social Learning Theory (SLT) which describes the conditions governing the occurrence of social learning. SLT emphasizes the importance of model-observer similarity in biasing social learning because, Bandura suggested, model-observer similarity increases the observer's identification with the model making it easier for the observer to relate modeled actions to his or her own (Bandura, 1977). More recent studies in fields ranging from sports psychology (Vescio et al., 2005) to health behaviors (Larsen et al., 2009; Perry et al., 1979) have continued to emphasize the importance of the similarity bias in cultural learning.

Both empirical and theoretical studies have suggested that another important model-based bias exists for high prestige individuals (Henrich and Gil-White, 2001). More broadly, Coussi-Korbel and Fragaszy (1995) stress the general importance of social dynamics such as egalitarianism and social dominance hierarchies in shaping model-biased cultural transmission. Laboratory experiments using the closed group method, in which information is circulated through a fixed group of individuals, have also found similarity and prestige biases and revealed an additional model-based biases for learning from successful individuals (Mesoudi and Whiten, 2008).

Content biases result in certain types of information being learned preferentially. Laboratory experiments using the transmission chain method, in which information transfer fidelity is measured among a group of people, have substantiated theoretical accounts of content biases. These studies have shown that counterintuitive information, gender stereotypes, social situations, and situations involving hierarchical relationships transmit with high fidelity (Mesoudi and Whiten, 2008).

Mental state attribution (a.k.a. Theory of mind)

Many cultural learning theorists argue that a unique human adaptation for culture is our sophisticated mental state attribution abilities

(Boyd, 2008; Tomasello, 1999; Tomasello et al., 1993a). During mental state attribution individuals develop ideas about the mental states of others and distinguish these mental states from their own. The ability to infer and subsequently encode the mental states of behavioral models during learning allows humans to modify cultural objects with their original purpose in mind. Iterative modification of cultural objects in turn creates a "ratchet effect" which allows for the summing of cognitive resources within and between generations (Tomasello, 1999).

Basic mental state attribution abilities emerge early in life and rapidly develop as the abilities for coordinated perspective-taking (intersubjectivity) and integrated perspective-taking (reflective intersubjectivity) come online (Tomasello et al., 1993a). Around the first birthday, human infants already recognize that other individuals have intentions as evidenced by their gaze-following and attention-sharing abilities (Tomasello et al., 1993a). Gergely et al. (2002) convincingly illustrate the intention understanding of 14-month olds by showing that they will only imitate a novel behavioral strategy when that strategy appears to be the most rational means to achieve a goal. By around 4 years of age, children recognize others as mental agents with thoughts different from their own (Perner et al., 1987). The ability of children to distinguish between their own thoughts and the thoughts of others is often explored using false belief tasks in which children have to predict the behavior of another individual based on that individual's false belief (Frith and Frith, 2003). The final developmental milestone of mental state attribution abilities occurs by 5 or 6 years of age when children are able to think about others reflecting on the beliefs of third parties (Sullivan, 1994). Mental state attribution abilities continue to improve into adulthood, with increasing social experience, and continue to constitute key elements of cultural learning.

Reward

Reward is another critical component of many types of learning including imitative learning, as described above, and cultural learning in general. Schultz (2006) defines the purpose of reward to be threefold: (1) induction of learning, (2) approach behavior for the reward itself, and (3) positive feelings associated with the reward and rewarded behavior. Rewards can be primary reinforcers (unlearned and culturally invariant), such as food and pleasant smells or secondary reinforcers (classically or instrumentally conditioned and culturally specific), such as money and attractive cars (Walter et al., 2005). Social stimuli such as smiling faces and cooperative behaviors are also powerful primary reinforcers (Walter et al., 2005).

Tomasello et al. (2005) suggest that the social situations inherent in cultural learning are powerful primary reinforcers and that the intrinsic reward value of cultural learning is a keystone of human cultural evolution. This means that the first time an individual engages in cultural learning, the experience is rewarding and thus the likelihood of learning and future learning is increased. While cultural learning in general may be rewarding, Castro and Toro (2004) suggest that the preferential learning of particular cultural information is dependent on the development of parental ability to approve or disapprove of offspring behavior. The child's sensitivity to both reward and punishment allows for preferential learning of correct, rewarded, behaviors over incorrect, punished ones. Castro and Toro (2004) suggest that this reward- and punishment-guided learning is a necessary addition to mental state attribution abilities in order for the ratchet effect to occur.

These three characteristics of human culture: learning biases, mental state attribution, and flexible reinforcement learning, when combined with humans' sophisticated imitative learning abilities, provide promising starting places for investigations into the neural architecture of human cultural transmission. The neural systems that subserve these functions are likely to play important roles in human cultural transmission.

Section II: candidate neural mechanisms of imitative cultural learning

A number of cognitive neuroscience studies have already identified neural systems underlying some of the key components of cultural imitative learning described above. In this section we review primate and specifically human cognitive neuroscience studies that investigate neural mechanisms associated with imitation and imitative learning, and model-based learning biases. We also briefly discuss how these neural mechanisms may implement mental state attribution and how they can potentially interact with neural systems processing reward.

The human mirror system, imitation, and imitative learning

Imitation learning is at the core of cultural learning and imitation learning processes have been well characterized behaviorally. Major cognitive neuroscience discoveries over the last decade have also given us a great deal of information about the neural mechanisms of imitation behavior. Recall that the ideomotor framework of imitation suggests that there is a common neural substrate for perception and action (Prinz, 2005). The mirror neuron system (MNS), first discovered in macaque monkeys using depth electrode recordings, has these perception-action coupling properties (Gallese et al., 1996). Neurons in the monkey's premotor cortex (area F5) (Gallese et al., 1996) and inferior parietal lobe (area PF) (Fogassi et al., 2005) fire both when the monkey performs a goal-directed action and when it sees a human or conspecific perform the same or a related action (Gallese et al., 1996).

Convergent evidence from a variety of imaging modalities, including fMRI, EEG, positron emission tomography (PET), transcranial magnetic stimulation (TMS), and most recently, single unit recordings (Mukamel et al., 2007) has suggested the presence of an MNS in humans (for a review see Iacoboni and Mazziotta, 2007). Putative human mirror neuron areas are present in the frontal lobe [posterior inferior frontal gyrus (piFG) and ventral premotor cortex (the human homologue of monkey F5)], and in the parietal lobe [rostral inferior parietal lobule (riPL)] (Rizzolatti and Craighero, 2004). Human studies have demonstrated brain responses compatible with mirror neuron activity while viewing and imitating object-oriented hand and foot actions (Buccino et al., 2001, 2004b), and hearing the sounds associated with these actions (Gazzola et al., 2006; Kaplan and Iacoboni, 2007). Additionally, the human MNS is also activated by viewing and imitating intransitive actions such as gestures (Iacoboni et al., 1999; Koski et al., 2003), mouth actions (Buccino et al., 2001), and facial expressions (Carr et al., 2003; Pfeifer et al., 2008).

Because mirror neurons provide a neural mechanism for pairing action observation and action execution, it has been hypothesized that the MNS is a key component of the neural substrate underlying imitation and imitative learning (Iacoboni, 2005; Iacoboni et al., 1999; Rizzolatti and Craighero, 2004). Iacoboni (2005) suggests, based on human neuroimaging and TMS data, that the core neural circuitry involved in human imitation consists of frontal and parietal MNS components as well as the superior temporal sulcus (STS). In this model, the STS gives rise to a higher-order visual description of the observed action, which is then fed into the MNS where the action's goal (piFG) and the motor plan to achieve the action (riPL) are coded. Finally, the predicted motor plan is fed back into the STS, where a comparison is made between the visual description of the action and the predicted sensory consequences of the imitative motor plan. It is at this point in the action-observation neural circuitry — when the observed and simulated motor plans are compared — that imitation accuracy and model-based cultural learning biases might be especially important. Presumably, the motor plans of self and other will be more similar in those cases where imitation accuracy and model-observer physical similarity is higher, though future studies will be needed to empirically test this hypothesis.

Iacoboni (2005) also proposes a model of the circuitry involved in imitative learning in which the aforementioned core circuitry communicates with the dorsolateral prefrontal cortex and motor preparation areas including the mesial frontal, dorsal premotor, and superior parietal regions. Though few neuroimaging studies of imitative learning have been conducted, the extant studies support the involvement of the MNS in imitation learning in general and support the imitative learning model proposed by Iacoboni (2005) in particular. In an fMRI study of observational learning of guitar chords by non-guitarists, Buccino et al. (2004b) found that the MNS and the above motor preparation areas were active. In a subsequent fMRI study, Frey and Gerry (2006) found more MNS activity when subjects observed complex hand action sequences with the intention to learn them and reproduce them later than when the same actions were viewed passively. Thus, the MNS is likely a key player in imitative learning of novel actions, a critical component of cultural learning.

The MNS and experience — could culture shape the MNS?

In addition to connecting executed and observed action, several studies discussed below indicate that activity of the MNS and interconnected regions is influenced by motor practice both in the short term (hours) and in the long term (years). Thus, the MNS may not only play a role in the acquisition of culturally mediated behaviors, but the MNS itself may be shaped by the presence of culturally mediated behaviors in one's motor repertoire.

Behavioral studies have demonstrated that action execution can be affected by previous experience observing related actions. For instance, Gillmeister et al. (2008) found that action imitation was facilitated by previous observation of task-irrelevant actions with the same effector; this priming effect was decreased by incongruent practice (observe foot and imitate with hand). Research using TMS has demonstrated that the behavioral effects of observational practice described above are directly mediated by the motor system. Stefan et al. (2008) had subjects practice thumb movements in the opposite direction of their baseline TMS-evoked thumb movements. The authors found that simultaneous movement execution and observation altered the direction of TMS-evoked thumb movements more than physical practice alone. Most intriguingly, Catmur et al. (2007) used an incongruent training strategy similar to Gillmeister et al. (2008) to create a "counter mirror" effect. After incongruent practice, observing the movements of one finger increased motor evoked potentials (MEPs) resulting from TMS in the finger paired during practice, rather than the same finger.

fMRI studies demonstrate that the behavioral and TMS-evoked practice effects described above are likely related to changes in MNS activity. Vogt et al. (2007) found increased activity in a number of brain regions (including putative mirror neuron areas) during observation of practiced versus nonpracticed guitar chords. On a longer timescale, Cross et al. (2006) demonstrate practice-related increases in MNS activity over the course of five fMRI scans at weekly intervals while subjects learned a novel dance sequence. Finally, Calvo-Merino et al. (2005) demonstrate that practice-related changes in MNS activity extend to real-world expertise built over many years. The authors find greater MNS activity when experienced dancers observe their own style of dance rather than a comparable but unfamiliar style. Collectively, these data suggest that daily experiences and those that extend over a lifetime, such as the practices of one's culture, have the potential to influence MNS function.

The MNS and model-based biases

In addition to playing a key role in human imitation, the MNS may represent the neural substrate of the similarity cultural learning bias, at least for the visuomotor aspects of similarity. Several studies have demonstrated that the MNS responds more intensely to the observation of conspecifics. For example, Buccino et al. (2004a) found that activity in the putative human MNS is modulated by model-observer similarity for the observation of biting actions of humans (greatest activity), monkeys (intermediate activity), and dogs (least activity). These species-dependent differences in MNS responses were even more pronounced for communicative actions (no measurable response for the dog barking action). This finding suggests that differences in physical appearance alone cannot explain these differential responses.

The MNS is also preferentially responsive to human biological motion. For example, Press et al.

(2006) compared subjects simultaneously observing and imitating human hands, human hands disguised to look like robotic hands, and actual robotic hands. The authors found that human hand observation, regardless of the hand's appearance, had a greater facilitatory effect on action performance than did robotic hand observation, even when the robotic and human hand were matched on size, color, and brightness (Press et al., 2006). Thus, human-like motion preferentially activates the MNS even when the effector is robotic. Gazzola et al. (2007) found MNS activity while subjects observed a robotic hand performing in a human-like fashion (by performing a variety of actions); however, neither Gazzola et al. (2007) nor Tai et al. (2004) found MNS activity when subjects viewed a robotic hand that was performing the same action repeatedly, which is less typical of human behavior. Intriguingly, Press et al. (2007) found that practice simultaneously observing and imitating a robotic hand abolished the human-biased action facilitation found pre-training, suggesting that human-biased activity in the MNS is, at least in part, the result of experience. Biological-motion related activity in the MNS extends to motion of the entire body. Ulloa and Pineda (2007) and Saygin et al. (2004) both found that the MNS responds to human actions represented by point-light walkers (moving groups of white dots representing the joints of a human) but not to the same stimuli when other dots were added to obscure motion the human form.

Current data suggest that the human MNS is also sensitive to more subtle aspects of model-observer physical similarity, such as ethnicity and gender, which may be more relevant cultural learning. For example, Molnar-Szakacs et al. (2007) found greater corticospinal excitability (a proxy for MNS activity, measured with TMS) in European American observers while they observed an ethnic in-group member versus an ethnic out-group member performing hand gestures, suggesting a positive relationship between MNS activity and model-observer similarity. In contrast, two other studies found more activity in the MNS when individuals viewed ethnic (Désy and Théoret, 2007) or gender (Cheng et al., 2006) out-group members, suggesting a negative relationship between MNS activity and model-observer similarity. Taken together, these data suggest that the MNS is sensitive to the visual similarity between model and observer at the level of species-typical appearance and biological motion, and in more culturally relevant domains such as gender and ethnicity. However, because of the variety of conclusions reached by these studies, and the potential role of experience in shaping MNS activity, the relationship between the degree of model-observer similarity and MNS activity remains unclear.

Neural mechanisms for mental state attribution

The cultural learning theories previously discussed (Tomasello et al., 1993a, 1999; Henrich and McElreath, 2003) propose that the ability to think about the intentions and mental states of others is critical for understanding the goal of observed actions. Intention understanding is thus vital for efficient and flexible imitative learning. After the discovery of mirror neurons, Gallese and Goldman (1998) proposed that the properties of these cells supported a simulation model of mental state attribution (simulation theory). Simulation theory assumes that we understand the intentions of others via a process of simulation, as if we were the other person. During simulation, the observation of another individual activates a similar suite of neural areas to when the observer performed the behavior himself "creat[ing] in the observer a state that resembles the target" (Gallese and Goldman, 1998). Indeed, subsequent studies in both monkeys (Fogassi et al., 2005) and humans (Iacoboni et al., 2005) suggested that mirror neurons are able to code the intention of an action, not simply the action itself. In Iacoboni et al. (2005) subjects were shown a hand picking up a cup, in one of two different contexts, a table set for tea, or the same table at the end of the meal. Despite the hand action being identical in both conditions, putative MNS regions demonstrated different levels of activity when the actions were viewed in the two different contexts. Thus, mirror neurons may implement not only imitation but also the function of mental state attribution in cultural learning.

Another model of mental state attribution assumes that we understand others' mental states by using an inferential process (Gopnik and Schulz, 2004). We observe the behavior of other people and then relate it to a set of folk psychology laws. By doing so, we can make theories about the mental states of other people as scientists make theories about the natural phenomena they study. From a functional standpoint, this inferential route to intention understanding does not map well onto the properties of mirror neurons. Indeed, a set of tasks typically used to study mental state attribution (the false belief task, the comparison of social interaction story listening to physical interaction story listening, and the comparison of viewing moving geometric shapes that depict social interactions to viewing randomly moving geometric shapes), consistently activate a set of neural regions that are not typically considered part of MNS: the dorsomedial prefrontal cortex (dmPFC), the posterior STS (pSTS), and the temporal pole (see Gallagher and Frith, 2003; Frith and Frith, 2003 for reviews). Activity in the pSTS area, however, is largely indistinguishable from the STS activations observed in imitation tasks (Iacoboni, 2005).

A number of individuals have proposed that the MNS and the above suite of brain areas (dmPFC, pSTS, and temporal poles) represent complementary neural systems underlying mental state attribution (Keysers and Gazzola, 2006, 2007; Pineda and Hecht, 2008; Uddin et al., 2007). For example, Keysers and Gazzola (2007) suggest the MNS provides a "pre-reflective" description of intention based on the visual description of a model's actions while cortical midline structures such as the dmFPC provide a "reflective" description of intentions based social introspection. Keysers and Gazzola (2007) suggest the inferential route to intention understanding may be especially important under circumstances when model-observer similarity is low or modeled behaviors were not previously present in the observer's repertoire, as is commonly the case during cultural learning. However, the interpretation of the activity in dmPFC in mentalizing tasks is rather difficult, due to the peculiar activation profile of this brain region (i.e., cognitive tasks result in signal decreases, rather than the typical signal increases, as compared to baseline activity; Iacoboni et al., 2004). Thus, it is at present unclear whether there is a distinct network for mental state attribution that relies on inferential mechanisms and that is anatomically located outside the MNS.

The reward system, sharing intentions, and imitation accuracy

The neural mechanisms of reward learning have been well mapped in animals ranging in complexity from *Aplysia* slugs (Hawkins et al., 1983) to rats (for a review see Schultz, 2006). Neural systems related to reward have been investigated in humans through the use of neuroimaging (for a review see O'Doherty, 2004). As is the case for the MNS, the current belief is that there is a putative reward system in the human brain encompassing brain systems homologues to the neural systems processing reward in animals. Three neural structures that are believed important in human reward processing are the ventral striatum, the nucleus accumbens, and the orbitofrontal cortex (OfC) (Hollerman et al., 2000; McClure et al., 2004; O'Doherty, 2004; Walter et al., 2005).

Reinforcement learning theory suggests reward is used to bias action selection and accordingly reward circuitry is often active during motor task performance (McClure et al., 2004). Significantly for the study of cultural learning, components of the reward network are also active during imitation. Activity in the lateral OfC was one of the main effects observed in the Chaminade et al. (2002) study of deferred imitation of Lego® assembly and a study by Williams et al. (2007) involving finger movement imitation. The lateral OfC activity in both of these studies was interpreted to reflect the uncertainty involved in producing the appropriate action as well as error monitoring between executed and observed actions, both functions suggested by Elliott, Dolan, and Frith (2000) to be reward-related. Lee et al. (2006) also found OfC activity during facial mimicry, perhaps related to the intrinsic reward value of viewing human faces (Walter et al., 2005).

In addition to the previous studies of generalized imitation, OfC activity has also been reported in studies comparing imitation or observation of actions with differing levels of familiarity to the subject. Jackson et al. (2006) report more OfC activity when subjects imitate models from a first person perspective than from a third person perspective. The authors attribute this activity to the increased similarity between imitation and observation in the first person perspective. Similarly, Calvo-Merino et al. (2005) find more OfC activity when dancers watch their own compared to an unfamiliar style. Elliott et al. (2000) suggest that the selection of stimuli on the basis of familiarity is related to the reward-related value of these stimuli. A more parsimonious explanation of these findings may simply invoke the role of OfC in inhibitory control (Elliott et al., 2000; Roberts and Wallis, 2000). For instance, dancers may have a stronger tendency to imitate, and therefore stronger need for motor inhibition, while watching the style of dance they typically practice. Future studies will have to disentangle the alternative hypotheses of reward processing and inhibitory control regarding the involvement of OfC in imitation.

Reward is also a central component of robotic models of human imitation, further highlighting the importance of reward in imitative learning. Mataric (1994) incorporate both vicarious reward and direct reward for conformity into their imitative learning algorithms used to drive social learning robots. Similarly, Atkeson and Schaal (1997) develop a robotic control strategy for single trial learning in which a reward function is learned from a demonstration and the behavior itself is acquired through trial and error learning.

Taken together, the neuroimaging studies discussed in this section highlight neural systems that play important roles in the cognitive mechanisms suggested by both theoretical and empirical work to be hallmarks of human cultural learning.

Section III: a model of the neural architecture of cultural imitative learning and future directions

We propose a tentative neural architecture of cultural imitative learning that has the MNS and associated imitative learning areas as its core. In our model, the reward network may support the motivation to imitate and reinforcement sensitivity important for cultural learning. MNS regions likely support mental state attribution through motor simulation (Koski et al., 2003). Under certain circumstances, medial prefrontal areas, typically considered "mentalizing" areas in the imaging literature (Frith and Frith, 2003; Gallagher and Frith, 2003), may also contribute to mental state attribution through an inferential route. Though tentative, the proposed cultural imitative learning circuitry generates testable hypotheses that future studies of cultural imitative learning can explore.

Future neuroscientific studies of imitative learning embedded in ecologically valid cultural contexts are needed to truly elucidate how the previously described neural systems (including those sub serving mental state attribution and reward processes) may function during real-world cultural imitative learning. In the remaining sections, we will discuss some future studies that will be required to further characterize the neural architecture of cultural imitative learning.

Future directions: the human mirror system and imitation

Though many neuroimaging studies of action execution, observation, and imitation have been conducted, relatively few studies of imitative learning of novel actions or action combinations exist to date (Buccino et al., 2004b; Frey and Gerry, 2006). Additionally, stimuli in existing imitation studies typically consist of photographs or videos of an isolated effector of a single individual performing simple movements against a blank backdrop. Though this type of reduction makes interpretation more straightforward, future studies investigating the role of imitation in cultural learning will need to employ more ecologically valid stimuli. By including the face, in addition to the acting effector, in action stimuli, important social information portrayed by the face can be utilized in action understanding. Facial information may change the way in which the action itself is processed and/or interpreted.

Action stimuli with increased complexity, such as action sequences rather than single actions, and increased social relevance, such as communicative actions directed toward others will more closely approximate the natural conditions in which cultural learning occurs. Finally, embedding imitation paradigms in a social context, such as imitative learning of the communicative gestures will also be useful in engaging neurocognitive mechanisms involved in cultural imitative learning.

Future directions: the MNS and model-based biases

The sensitivity of the MNS to aspects of model-observer similarity, such as ethnicity and gender, suggested by several studies (Cheng et al., 2006; Désy and Théoret, 2007; Molnar-Szakacs et al., 2007), may underlie the well-documented cultural learning biases for self-similar individuals (Bandura, 1977; Henrich and McElreath, 2003; Mesoudi and Whiten, 2008). These studies have examined model-observer similarity only in the context of action observation. No studies to date have addressed model-observer similarity during imitation or imitative learning. Furthermore, whether there is a positive or negative correlation between model-observer similarity and MNS activity in terms of ethnicity and gender remains unclear from present studies.

Other socially salient physical characteristics such as age, socioeconomic status (as reflected in physical appearance), as well as action quality and model-observer familiarity should also be considered in the context of neurobehavioral investigations of cultural learning. A final point concerns the relationship between the physical and nonphysical elements of social characteristics such as gender, ethnicity, and age. In order to determine which aspects of similarity — physical/bottom-up or social/top-down — influence brain activity during imitation, it will be necessary to design studies in which the physical appearance of observed models and social information can be disassociated.

Future directions: the MNS, mental state attributions, and the reward system

It is clear that mental state attribution abilities are of central importance for cultural imitative learning. However, the question of whether mental state attribution is achieved via simulation mechanisms supported by the MNS, "mentalizing" mechanisms supported by neural regions including the dmPFC, or some integration of these two remains unanswered. The use of tasks that differentiate between simulative and inferential mechanisms during imitation will be useful in identifying the neural substrates of mental state attribution during cultural imitative learning.

The human reward system is critical for learning and is some times active during action observation and imitation. Cultural learning theory suggests that reward is important for the motivation to learn imitatively, for sharing intentions, as well as for learning behaviors accurately. A next step in elucidating the role of reward circuitry in human imitative learning will be to investigate the neural basis of imitation and imitative learning of directly and vicariously rewarded actions. Comparison of tasks when motivation to imitate differs, such as virtual food retrieval tasks in hungry and sated subjects as in Dorrance and Zentall (2001), will be useful for determining the role of motivation in the neural basis of cultural imitative learning.

Conclusion

Cultural learning theory suggests that imitation, mental state attribution, and reinforcement learning are key cognitive mechanisms underlying human cultural learning. Cognitive neuroscience studies provide insight into the neural systems associated with these functions. Thus, anthropology and cognitive neuroscience provide the neuroscientific study of cultural learning a head start. However, many studies of imitation learning in cultural contexts that will engage mental state attribution and reinforcement learning will be needed to fully explore and explain the neural architecture of cultural imitative learning.

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CHAPTER 13

The cultural neuroscience of person perception

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Abstract: In the last few years, theorists have argued that culture can shape processes of basic visual perception. This work has primarily focused on cultural influences in nonsocial domains, such as cross-cultural differences in seeing and attending to focal stimuli versus backgrounds. Recently, researchers have begun to examine how culture can shape processes of social perception. We review such evidence and describe how culture tunes both the outcomes of social perception (as revealed in behavioral responses) as well as the activity of the neural mechanisms that mediate these outcomes. Such evidence comes from the domains of emotion recognition, social status perception, social group evaluation, and mental state inference. We explicate these findings through our viewpoint that ecologically important aspects of the sociocultural environment shape perceptual processing and its neural basis. More broadly, we discuss the promise of a cultural neuroscience approach to social perception and some of its epistemological challenges as a nascent interdisciplinary enterprise.

Keywords: culture; psychology; neuroscience; perception; behavior; social status; face; emotions

Humans are biological phenomena. We are made up of cells, hormones, and genes; we have a nervous system and neurons within it. All our perceptions, cognitions, and behaviors have a biological basis; they are instantiated in the brain and body. Yet, we are also sociocultural phenomena. We see, think, and act in the context of others, within a society and culture, in particular times and spaces, among environments where specific meanings, practices, and institutions arrange and determine our everyday lives. Over the past few decades, a growing number of psychologists, sociologists, and anthropologists have stressed that many of taken-for-granted ways of perceiving and interpreting ourselves and the world around us — as much as we like to ethnocentrically universalize them across time and space — are in fact culturally and historically specific (e.g., Berger and Luckmann, 1967; Shweder, 1990; Triandis, 2007). This work has pointed out that our quotidian realities and basic ways of perceiving, thinking, and acting are often constructed by the cultural and ecological context that constitutes them.

The notion that psychological processes are shaped by culture, though a central tenet in the field of cultural psychology, has received a lukewarm reception by the broader field of experimental psychology. As many have noted (Shweder, 1990; Spivey, 2007), research in experimental psychology and cognitive science generally understands the mind to be akin to a digital computer or central processing unit (CPU), employing operations that are insulated from context, independent of content, and certainly unfettered to culture. The job of such research is

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to characterize these various operations, which are assumed to be universal among humans, with as much possible depth and detail. Cultural variation is thrown into the lump of human variation, which is considered random noise that researchers attempt to minimize through tightly controlled laboratory experimentation. The overarching hope is that they may gain a view into the underlying human CPU and the universal and natural laws that govern it. In this way, the argument that culture can construct and constrain psychological processes is a perspective generally disregarded by mainstream psychology and the neurosciences. Although the plasticity of neural systems and their modulation by accumulated experience has long been documented, neuroscientists continue to focus on characterizing the fundamental neurobiological substrates of human cognition, which are implicitly assumed to be universal and therefore unperturbed by culture (Han and Northoff, 2008).

By contrast, new perspectives in cognitive science, such as externalism, embodied cognition, and a dynamical systems account of the mind have permitted researchers to understand mental processes as emergent properties of a self-organizing cognitive system straddled among the interactions of brain, body, and the surrounding environment (Spivey, 2007). Although the field of cultural psychology may not formalize such a dynamical systems approach, the premise that mind and culture are mutually constituted and engage in constant interaction over time is taken as a theoretical given and empirical starting point (Heine, 2008). One of the most pressing questions for the discipline of cultural psychology is parsing out which mental processes are universal and which display cultural diversity, ultimately toward a more complete understanding of the nature of human variation (Chiao and Ambady, 2007). By integrating these questions with a biological perspective, the burgeoning field of cultural neuroscience permits a fuller understanding of mental phenomena at multiple levels of analysis.

We, in particular, stress that cultural neuroscience can do much more than merely identify and distinguish the neural correlates of universal versus culturally sensitive psychological processes. We believe that cultural neuroscience can serve to constrain psychological theory and make novel insights about cultural influences on mental processes, which would otherwise be unrealizable without knowledge of how the brain works (i.e., neuroscientific models) and the tools to inspect it (e.g., neuroimaging). We suggest that by knowing about the nature of neural systems, cultural neuroscientists can advance novel and nuanced predictions about how culture might (or might not) influence these systems and the mental processing they subserve. Moreover, by investigating the influences of cultural factors in tandem with predeterminate conditions — such as genetic factors — via neuroimaging and genomic imaging methods, the emerging field of cultural neuroscience promises a more complete understanding of mental phenomena and their dynamic interactive nature (genes ↔ brain ↔ culture). That is, cultural variation may come into being from the multilevel interactions between genes, brain, and culture (Bonham et al., 2005; Chiao and Ambady, 2007). As both biological and sociocultural creatures, our mental system is highly interactive, evolving over time as a function of changes in genetic and biological material in addition to changes in our sociocultural context, and their many interactions. Cultural neuroscience offers an exciting multilevel approach to precisely characterize how processes of this dynamic mental system emerge through a complex interplay between genetic, neural, and cultural forces.

Perception as cultural affordance

Why might culture influence perception? Should not the human perceptual system have adapted to take up the sensory information out in the world as accurately and efficiently as possible, regardless of culture? Not so. In the ecological approach to visual perception, J.J. Gibson made an important argument: perception is for action (Gibson, 1979). That is, visual perception always operates in some ecological context that marks some set of potential behaviors for the perceiver. Perception is intrinsically tied to a stimulus's *affordances*: the interaction possibilities between a perceiver and the target stimulus. Gibson argues: "Any substance, any surface, any layout has some affordance for benefit or injury to someone. Physics may be value-free, but ecology is not" (Gibson, 1979, p. 140). The human perceptual system evolved for seeing the world in terms of what the world *affords* the perceiver, that is, for perceiving useful action possibilities to operate on it. An important consequence of this is that each of us perceives a different world. If perception exists for action possibilities with the environment, then each animal, given its unique animal–environment interactions, perceives the environment in a different way. The same surface in ambient light is perceived by the human as *something to walk on* as it is by the dog as *something to leap onto*. Or, the same handle bar is perceived by the human as *something to grab* as it is by the dog as *something to bite*. Thus, there is an ecological value — an affordance value — embedded into the objects and surroundings of our perceptible worlds.

If we perceive stimuli by way of what they afford us, then, to be sure, culture should influence perceptual processes. This is because the systems and practices of one's culture largely determine the function and value of stimuli in the environment and what these stimuli afford individuals (their affordance value).[1] For instance, in the United States, a jagged rock in the middle of a stone driveway is a useless impediment, something to kick away or remove. In a small village society, however, the same jagged rock may be something to pick up, grab firmly, and lunge into an enemy or prey to kill. According to an ecological perspective, members of these two cultures should therefore attend to and literally see this jagged rock stimulus in very different ways, as it affords divergent culturally tuned possibilities (Norman, 1988). Thus, culture can serve as an ecological context in which affordances in the sociocultural environment (e.g., social structures, ideas, rituals, practices, orientations) fundamentally shape perceptual processes and evoke culturally specific perceptual, cognitive, and motivational responses (also see Kitayama and Markus, 1999).

Cultural impact on nonsocial perception

Two cultures whose social structure and practices differ considerably in a way that is likely to influence perceptual processing are what are regarded as Western culture and East Asian culture. Western societies are characterized by independence and individualism, emphasizing individuals' goals and achievements. East Asian societies, on the other hand, tend to be more interdependent and collectivist, emphasizing relationships and roles. These two different sociocultural systems are known to give rise to dissimilar patterns of cognition (Nisbett et al., 2001). Recent work has shown that these systems are also likely to influence visual attention to aspects of the environment (e.g., Kitayama et al., 2003; Masuda and Nisbett, 2001). Specifically, practices and ideas in Western societies tend to require separating objects from their contexts and interpreting independent and absolute aspects of environmental stimuli (i.e., analytic thinking). Practices and ideas in East Asian societies, however, tend to require interpreting objects in conjunction with their context and understanding the relatedness among environmental stimuli (i.e., holistic thinking). Thus, we can say that in East Asian societies (emphasizing interdependence), there is more perceptual affordance for interrelatedness among visual stimuli and surrounding contexts. If true, East Asians should direct more attention to these. In contrast, Western societies (emphasizing independence) place more affordance value on salient objects and one's own relationship to those objects. This should lead to Westerners directing more attention to these, without as much concern for context.

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[1] Admittedly, Gibson's (1979) original formalization of the concept of affordance does not extend perfectly to "perceived" or more abstract capabilities in a sociocultural environment. His concept of affordance is dependent only on the physical capabilities of an animal, not their goals, values, prior knowledge, or culture. Such "perceived affordances" or "cultural affordances" are formalized in later work by scholars such as Norman (1988) and Kitayama and Markus (1999).

Indeed, several studies have converged on this exact pattern of results.

Overall, Americans engage in more analytic perception and Japanese engage in more holistic perception. For instance, Americans are better at recognizing changes in focal objects, whereas Japanese individuals are better at recognizing changes in contexts (Masuda and Nisbett, 2001, 2006). The framed-line test (Kitayama et al., 2003) has been especially useful in demonstrating how these two cultures shape divergent patterns of visual perception and attentional deployment. In the framed-line test, participants are shown a square figure with a vertical line hanging from its top edge (but not spanning the entire height of the square), located in the horizontal center. After briefly inspecting this arrangement, participants are shown a new square figure of a different size. In the absolute condition, participants are asked to draw a line in this new square that is identical in absolute length to the vertical line previously seen. In the relative condition, however, they are asked to draw a line that has identical proportion to the context (i.e., the surrounding square frame) as that of the vertical line previously seen. Thus, performance in the absolute task depends on analytic processing of a salient stimulus and characteristics that are independent of context. Performance in the relative task however depends on holistic processing that includes the surrounding square frame, and the relationship between the salient stimulus and its context. Consistently, Americans perform better in the absolute task than in the relative task, whereas Japanese show the reverse pattern, performing better in the relative task than in the absolute task (Kitayama et al., 2003). Thus, Americans tend to allocate attention analytically (to salient stimuli and context-independent characteristics) whereas Japanese, in contrast, tend to allocate attention holistically (to the context and interrelationships among various objects in view).

To characterize the neural basis of this cross-cultural difference in attentional deployment, Hedden et al. (2008) had American and East Asian participants take a modified version of the framed-line test while blood oxygenation level–dependent (BOLD) responses were measured using functional magnetic resonance imaging (fMRI). For both Americans and East Asians, culturally nonpreferred judgments (i.e., relative judgments for Americans and absolute judgments for East Asians) engaged a constellation of frontal and parietal brain regions involved in attentional control, including the left inferior parietal lobule and the right precentral gyrus, relative to culturally preferred judgments (i.e., absolute judgments for Americans and relative judgments for East Asians). The culture-dependent activation of this attentional network was interpreted as reflecting an increased need for attentional control when individuals made judgments that required a processing style for which they were less culturally prepared. Moreover, within each culture, the degree to which culturally nonpreferred judgments selectively engaged this attentional network correlated with individual differences in how much participants identified with their culture and endorsed its values. For instance, when making absolute judgments, the more an American self-reported being more independent, the less this attentional network was engaged (and thus, the more he or she was culturally prepared to make these judgments). Similarly, when making absolute judgments, the more an East Asian self-reported being ingrained into American culture, the less this attentional network was engaged.

In sum, one's cultural background determines the engagement of a frontoparietal attentional network when making basic perceptual judgments. Moreover, this engagement is sensitive to individual differences in how much an individual subscribes to a particular culture or is acculturated in it. Thus, divergent aspects of the American and East Asian sociocultural environments shape American and East Asian perceivers with different attentional strategies and, correspondingly, different patterns of activity in a frontoparietal network involved in deploying these strategies. This demonstrates how culture equips its perceivers with culturally tuned perceptual processes to better navigate their cultural worlds. Moreover, this tuning is manifest both in perceptual outcomes (e.g., accuracy data) and in the functional activity of brain mechanisms that mediate such outcomes.

Cultural influences on perceiving other people

From an ecological perspective, other people who afford social interaction are some of the most, if not *the* most, important objects of the environment to be perceived. As J.J. Gibson noted, "the richest and most elaborate affordances of the environment are provided by other animals and, for us, other people" (Gibson, 1979, p. 135). It is difficult to imagine an instance of perception more crucial than the imperative to perceive others. This is because such perceptions are inextricably bound to social affordances, as the visual construal of person characteristics is very likely to bear ecologically important consequences, such as lasting judgments, evaluations, and interpersonal interaction (McArthur and Baron, 1983). These characteristics may include other individuals' gender, race, ethnicity, age, cultural membership, emotional status, and social status, among others.

Recognizing emotions

Successfully reading others' emotions is important because they avail the perceiver with information about another's behavioral readiness and information about the environment. For instance, emotional expressions signal upcoming behaviors (e.g., anger: *I am going to fight you*) or environmental conditions (e.g., fear: *Danger is nearby*). As others' facial expressions warn and ready perceivers for impending action, and because such actions are most likely to happen within one's culture, the emotions that are most ecologically relevant are those that are expressed by members of one's own culture (Weisbuch and Ambady, 2008). Indeed, it has been proposed for over two decades that one's cultural background may influence the recognition of others' emotions (Lutz and White, 1986). Thus, one question of interest to social and cultural psychologists is whether members of a given culture exhibit a selective ability to recognize the emotions of members of one's own culture. It is possible that acculturation leads to the unique tuning of the perceptual system to emotional expressions of other members of that same culture. Elfenbein and Ambady (2002) conducted a meta-analysis of studies involving face emotion recognition tasks across multiple cultures. Indeed, analysis of the results from these studies led to the conclusion that individuals are better at recognizing own-culture expressions relative to other-culture expressions, pointing to a robust cultural specificity in emotion recognition.

To investigate the neural basis of this cultural specificity in recognizing facial emotion, Chiao et al. (2008) conducted an fMRI study with American and native Japanese participants. Participants were presented with American and Japanese faces expressing fear, anger, joy, or nothing (neutral affect). Behaviorally, Americans were more accurate at judging own-culture emotions relative to those of the other culture. Similarly, Japanese individuals, although not reliably more accurate, were quicker to judge own-culture emotions relative to those of the other culture. This thus conformed to Elfenbein and Ambady's (2002) conclusion of a cultural specificity in emotion recognition. This cultural specificity was reflected by brain activity as well. Chiao et al.'s (2008) neuroimaging results revealed that own-culture fearful faces elicited greater activity in the bilateral amygdala relative to fearful faces of the other culture. Notably, this own-culture selectivity was found only for fear faces, not faces expressing neutral affect, anger, or joy. This is fitting given that others' fear is a social signal that is extremely adaptive and probably carries the most ecological importance among all emotions. We argued earlier that cultural influences on perception are likely to center around what affordances the perception provides. Chiao et al.'s (2008) findings are consistent with our view, finding cultural specificity in amygdala activity only for the most ecologically relevant stimuli (fear faces of one's own culture).

Although the role of the amygdala in responding to fear expressions is often interpreted as the direct detection of negative affect or threat, it has long been known that the amygdala does not necessarily process valence per se, but is instead driven flexibly by a stimulus's motivational importance (Phelps and LeDoux, 2005). For instance, the amygdala responds to both negative and positive stimuli, so long as the stimuli are subjectively valued and predictive of a social evaluation (Schiller et al., 2009) or relevant for individuals' current processing goals (Cunningham et al., 2008). Thus, stronger responses to own-culture fearful faces need not necessarily be interpreted as these faces directly signaling more threat with the amygdala detecting this stronger signal (e.g., Davis and Whalen, 2001; Glascher and Adolphs, 2003). Instead, it is possible that the amygdala's selective responses to own-culture fearful faces reflect the fact that these faces carry more motivational significance (see Weisbuch and Ambady, 2008, for the motivational significance of own-culture fear). Specifically, selective responses to own-culture fearful faces (relative to other-culture fearful faces) likely reflect the amygdala's enhancement of the perception of motivationally significant stimuli (i.e., Anderson and Phelps, 2001) or heightening of a physiological preparedness to motivate rapid action (i.e., Phelps and LeDoux, 2005) in response to the fear of own-culture allies. These interpretations would be consistent with our argument that cultural influences on social perception, and the neural mechanisms subserving them, are likely to be driven by what affordances or action possibilities are availed to perceivers.

Values in perception: dominance and subordination

Beyond recognizing others' emotions, we often see their social status as well, as it is readily revealed by the face and body (Hall et al., 2005). Because many cultures are organized by social hierarchy, others' social status affords perceivers valuable information and determines behavioral consequences. It is cued by signals of dominance (marking higher status) and signals of subordination (marking lower status), which are conveyed effortlessly by bodily expressions (Hall et al., 2005). Although these cues are recognized with considerable consistency across cultures (e.g., Bridge et al., 2007), cultures can greatly differ in how they assign value to these cues. For instance, in the United States, there is more affordance to be dominant, as dominant thinking and behavior is positively reinforced. Americans are encouraged to be independent, self-elevating, assertive (e.g., Moskowitz et al., 1994), and to climb the hierarchy (Triandis and Gelfand, 1998). Dissimilarly, in Japan, there is more affordance to be subordinate, as subordinate thinking and behavior is positively reinforced. Japanese individuals are encouraged to be sociable and cooperative (Moskowitz et al., 1994), to be affiliative rather than competitive (Yamaguchi et al., 1995), and to show obligation to others (Oyserman et al., 1998). In short, American culture generally encourages dominance, whereas Japanese culture generally encourages subordination.

When an American or Japanese individual perceives another dominant or subordinate person, several things need to occur. Among these is that the brain must represent this stimulus's culturally learned value or significance. That is, on seeing other people who are dominant or subordinate, perceivers must implicitly recognize the culturally learned value associated with dominance or subordination. One particular circuit of brain regions, the mesolimbic reward system, has long been known to be involved in these value representations. By detecting and representing the value of motivationally important stimuli, both positively rewarding or negatively aversive, the mesolimbic reward system can ultimately motivate behavior — even complex social behavior (Knutson and Wimmer, 2007; Schultz, 2000). Thus, it seems plausible that cultural influences on dominant and subordinate behavior may be realized by way of the mesolimbic reward system.

We investigated this in an fMRI study involving American and native Japanese participants (Freeman et al., 2009). In the scanner, participants were presented with images of dominant bodies and subordinate bodies depicting only figural outlines, which removed cultural membership cues and preserved only nonverbal information about social status. After the scan, we assessed behavioral tendencies toward dominance or subordination using a questionnaire (e.g., "I impose my will on others" or "I let others make the decisions"). As expected, behavioral results indicated that Americans exhibited a greater tendency for dominant behavior, whereas Japanese exhibited a greater tendency for subordinate behavior. Neuroimaging results revealed, in Americans, that the head of the caudate nucleus and the medial prefrontal cortex (mPFC), two important components of the mesolimbic reward system, showed stronger responses to dominant stimuli (relative to subordinate stimuli), whereas in Japanese, these regions showed the reverse pattern: stronger responses to subordinate stimuli (relative to dominant stimuli). Moreover, activity in the right caudate and mPFC correlated with individual behavioral tendencies toward dominance versus subordination: stronger responses in the caudate and mPFC to dominant stimuli were associated with more dominant behavior and stronger responses in the caudate and mPFC to subordinate stimuli were associated with more subordinate behavior.

Thus, perceiving dominance and subordination in others elicited responses in the caudate and mPFC congruent with these behaviors' culturally learned reward value, and the magnitude of these responses predicted individuals' tendencies to take on related social behavior. This finding demonstrates how the cultural tuning of tendencies in social behavior can be accomplished by way of the mesolimbic reward system. Clearly, culture places value on certain behaviors or practices. We found that this culturally learned value is represented in the caudate and mPFC. Importantly, mesolimbic representation of this culturally learned value can be automatically triggered in contexts involving the perception of other people, highlighting the role of neural representations of culturally learned values during social interaction.

Evaluating social groups

Another way in which culture can shape social perception is through molding individuals' implicit associations about social groups. For instance, American culture has a long history of harboring negative associations about Black people. Given how culturally prevalent these negative associations about Black people are, they are likely to be automatically triggered when individuals confront any novel Black individual. Indeed, a long line of work in social psychology confirms that such automatic evaluation is likely to occur (Fazio et al., 1986, 1995), and several fMRI studies have supported this idea as well.

In one study, White Americans were subliminally presented with White and Black faces while brain activity was measured using fMRI (Cunningham et al., 2004). Relative to White faces, subliminally presented Black faces evoked a stronger amygdala response, which was interpreted to reflect the automatic processing of a negative culturally learned association with Black people. In a later study, this amygdala response to Black faces was extended to supraliminal presentation as well (Lieberman et al., 2005). In addition, although not replicating an overall stronger amygdala response to Black faces, Phelps et al. (2000) found that the degree to which White Americans' amygdala responds to Black faces correlates with variation in how much an individual harbors an implicit negative association with Black people. This finding thus directly ties White Americans' amygdala responsiveness to Black faces to implicit bias against Black people.

An alternative interpretation, however, is that rather than reflecting culturally learned associations about Black people, amygdala responses to Black faces reflect a more generalized automatic evaluative response to out-group members. Inconsistent with this, however, Lieberman et al. (2005) found that Black American participants also showed greater amygdala responses to Black faces relative to White faces (converging with the White Americans' pattern of results), suggesting that amygdala responses reflect culturally ingrained attitudes, not a simple out-group effect. Moreover, Phelps et al.'s (2000) correlation between amygdala responses to Black faces and individual differences in culturally learned associations about Black people support this view as well. It is worth noting, however, that Lieberman et al.'s (2005) findings need not be interpreted as Black Americans' internalization of culturally learned associations about their own social group; it could simply reflect that other Black faces have more motivational importance for Black Americans (see above, and Phelps and LeDoux, 2005), a hypothesis that future research will need to test directly. In short, culturally learned attitudes about social groups endow perceivers with an automatic evaluative response, mediated by the amygdala, to members of those social groups.

Inferring mental states from the eyes

Last, we turn our attention to cultural influences on inferring others' mental states. The ability to infer others' mental states is one of the most prominent characteristics that distinguishes humans from other animals (e.g., Saxe and Baron-Cohen, 2006) and is often referred to as "theory of mind." Cross-cultural studies of theory of mind have reported universality for interpreting others' mental states. Avis and Harris (1991) showed that children in both literate and preliterate cultures develop mental state inference within the same developmental window. Similarly, adult members of literate and preliterate cultures appear to express the same level of ability for inferring others' thoughts (Sugiyama et al., 2002). Kobayashi et al. (2006) provided neuroimaging evidence for cross-cultural universality in theory of mind, implicating areas such as the temporoparietal junction and mPFC, which appear to be invariant to culture. However, these studies used false-belief tasks, which rely on making inferences about others' mental states based on verbal descriptions of a target's behavior.

Another important way in which we infer others' mental states, however, is by the subtle cues that they exhibit in their facial expressions. An often-used assessment of this kind of mental inference is the "Reading the Mind in the Eyes" test (RME; Baron-Cohen et al., 2001). The RME presents individuals with photos of individuals' eyes and several adjectives that may or may not describe the individual's mental state. The test involves choosing which adjective is most appropriate to describe the mental state of the person in the photograph. Individuals with an intact capacity for mental inference show high agreement for the adjectives they choose in describing the targets' mental states. Individuals who lack mental inference abilities, such as patients with neurological damage, show severe impairment in choosing which adjectives best describe the targets' mental states (Adolphs et al., 2002).

Recent work has shown that culture influences individuals' performance on the RME. This would make sense given that the mental states of one's own culture are likely to be more ecologically significant than the mental states of a different culture (see above, and Weisbuch and Ambady, 2008). Using both the original Caucasian-face RME developed by Baron-Cohen et al. (2001) and an analogous, Asian-face RME developed for their study, Adams et al. (2009) found that American participants performed better with the Caucasian RME and that Japanese participants performed better with the Asian RME. Such results were mirrored in neural activity as well. Adams et al. (2009) found that own-culture RME judgments (relative to those of the other culture) selectively engaged the superior temporal sulcus (STS), a brain region important for theory of mind. Specifically, American participants showed stronger bilateral STS activity when inferring the mental states of American targets, as opposed to Japanese targets, and Japanese participants showed stronger bilateral STS activity when inferring the mental states of Japanese targets, as opposed to American targets. Thus, culture equips its perceivers with a culturally tuned ability to infer others' mental states. This is manifest both in behavioral outcomes in the accuracy of making these mental inferences and in the activity of the STS, which helps mediate these inferences.

Conclusions

As we attempted to articulate throughout this chapter, the emerging field of cultural neuroscience promises a fuller understanding of social perception. We reviewed evidence showing that culture shapes basic perceptual processes across nonsocial and social domains. We highlighted how these cultural specificities are manifest both in ultimate perceptual outcomes (as indexed by accuracy or response latencies) and in the activity of the neural mechanisms that mediate those outcomes. We stressed our argument that affordances in the sociocultural environment (i.e., ecologically and motivationally significant ideas, practices, social structures, among many others) are likely to shape perceptual processing and give rise to culturally specific behavioral and neural responses. Much of this research involved identifying the neural correlates of established cross-cultural differences in perception, cognition, and behavior. We believe this work is extremely important, but as suggested earlier, we look forward to cultural neuroscience work that uses neuroscientific models to constrain psychological theory and advance new understandings of cultural influences on mental processes that are otherwise unrealizable without knowledge of how the brain works and the tools to inspect it.

It seems unassailable at this point that the adult human brain is a place where plasticity is the norm, not the exception. This is a point that has startled some neuroscientists and psychologists, who have generally privileged anatomical and functional fixity (Spivey, 2007). As one neuroscientist said, writing in *Science*: "If the neural systems used for a given task can change with 15 min of practice … how can we any longer separate organic structures from their experience in the organism's history?" (Posner, 1993, p. 674). The field of cultural neuroscience should answer with a resounding: *we cannot!* The epistemological stripping of the brain from its environment, social context, culture, and ecology — a notion that pervades the fields of psychology and neuroscience — has provided major challenges for the emergence of a research field dedicated to the study of the interactions between brain and culture, between the neural and the ecological. We hope that by studying how the brain and culture interact, the burgeoning field of cultural neuroscience can move beyond these dichotomies and provide novel insights into psychological processes. This is especially true for the cultural neuroscience of social perception, given the dynamic and interactive nature of perceiving and interacting with others (e.g., Freeman et al., 2008; Johnson and Freeman, 2009).

Abbreviations

BOLD	blood oxygenation level–dependent
CPU	central processing unit
fMRI	functional magnetic resonance imaging
mPFC	medial prefrontal cortex
RME	Reading the Mind in the Eyes
STS	superior temporal sulcus

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CHAPTER 14

Understanding the self: a cultural neuroscience approach

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Abstract: The self has been addressed extensively by philosophers and psychologists from different cultures. Recent cognitive neuroscience studies have uncovered neural substrates underlying the processing of different aspects of the self. As social psychologists have shown evidence for differences in self-construal styles between Western and East Asian cultures, recent transcultural neuroimaging research sought to find potential neural mechanisms mediating cultural specific self-related processing. The findings of transcultural neuroimaging research help to understand the culture-dependent nature of the self and its underlying neural substrates. This also sheds light on how to conceptualize the self in psychological and philosophical terms.

Keywords: culture; neuroimaging; self; medial prefrontal cortex

Introduction

Understanding the self has been one of the most salient problems throughout the history of philosophy and psychology (Gallagher, 2000; Northoff, 2004; Zhu and Han, 2008). For example, William James distinguished between a physical self, a mental self, and a spiritual self. These distinctions seem to reappear in recent self-concepts discussed in neuroscience. Damasio (1999) and Panksepp (1998; 2003) suggest a "proto-self" in the sensory and motor domains, respectively, which resembles James's description of the physical self. Similarly, what has been described as the "minimal self" (Gallagher, 2000) or "core or mental self" (Damasio, 1999) might correspond more or less to James' concept of mental self. Finally, Damasio's (1999) "autobiographical self" and Gallagher's (2000) "narrative self" strongly rely on linking past, present, and future events with some resemblances to James' spiritual self.

The distinct self-concepts differ in the class of stimuli and their specific material or content reflecting what is called different domains. The "proto-self" refers to the domain of the body whereas the "autobiographical self" reflects the domain of memory. Other self-concepts like the emotional self (Fossati et al., 2003), the spatial self (Vogeley and Fink, 2003), the facial self (Keenan and Nelson, 2001), the verbal or interpreting self (Turk et al., 2003), and the social self (Frith and Frith, 1999, 2003) refer to further domains. Recent neuroimaging research of neural correlates of self

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highlights the role of cortical midline structures (CMS) in self-related processing (Northoff and Bermpohl, 2004; Northoff et al., 2006). Most of the imaging studies implicitly presuppose a concept of the self as self-consciousness or self-awareness (see Gusnard et al., 2001; McKiernan et al., 2006). Various tasks applied in these studies required subjects to make explicit reference to some aspects of themselves and to consciously access and monitor representational content about one's self, that is, conducting self-referential processing. Self-referential processing consists of consciousness or awareness of the self and is supposed to involve higher-order cognitive function, out of which the self emerges at the pinnacle of the psychological and neural hierarchy. At the philosophical level, such higher-order view of self-referential processing corresponds to predominantly cognitive and higher-order accounts of the self. The characterization of the self as higher-order cognitive function is however not compatible with the alleged domain-independence of the self. Our recent meta-analysis showed that self-related processing remains domain-independent, that is, occurring across various domains, be it verbal, facial, spatial, or even sensorimotor, each time recruiting the CMS (Northoff et al., 2006). If so, the self cannot be characterized as higher-order cognitive functions because then one would expect no occurrence of the self in the lower-order domain of sensorimotor functions.

What, however, is self-related processing? We assume that self-related processing provides a special code, format, or mode by means of which sensory, emotional, or cognitive stimuli become oriented toward and associated with the respective person. This may be tested empirically by investigating the relationship between self-relatedness and sensory processing. We would postulate that the latter is guided implicitly by the former. What does this imply for the concept of the self? If self-related processing is indeed a special kind of format or code, self-related processing should be implicated in all kinds of processing in a very basic sense rather than emerging as higher-order cognitive or metacognitive function at the pinnacle. If this is true, self-relatedness codes, formats, and consecutively determines the mode in which all incoming stimuli, be they extero- or interoceptive, are processed by our brain. Though we can seemingly not escape from self-relatedness, we are apparently at least able to modulate our reactivity toward it by means of cognitive modulation. Cognitive modulation allows us to distance ourselves from our own self by, for example, self-awareness or self-consciousness where one takes an observing or analytical perspective (rather than an experiential one) on one's self. Self-relatedness can then no longer be regarded as the output of some higher-order cognitive function but rather the input to the latter that aims to control and modulate it. In this case, self-relatedness is no longer higher-order function among others like working memory, attention, etc., but rather a very basic function that predisposes and determines higher-order functions.

This characterization of self-relatedness as basic formatting and organizing functions entails the following empirical predictions. First, one would expect close relationship between self-related processing and social processing, since self-relatedness should then modulate and impact all incoming stimuli from the social environment. Second, one would expect neural overlap between self and other with both no longer mutually exclusive and contradicting each other with regard to their neural correlates. Third, self-related processing as basic and formatting function should occur in an implicit and automatic mode. Indeed, these features of self-related processing have been well observed in recent transcultural neuroimaging research.

Because the self of each individual develops in a specific sociocultural context, it may undergo strong modulations of social contexts and cultural values and formulate a particular style to adjust the way to efficiently interact with other individuals in social environments. Indeed, social and cultural psychologists have shown ample evidence for cultural difference in the self and self-related processing (Markus and Kitayama, 1991; Zhu and Han, 2008). The findings of social and cultural psychology raise further interesting questions of whether neural representation of the self and neural substrates of self-related processing are shaped by socio-cultural contexts. Moreover, as the self can be divided into different domains, one would further expect to observe cultural influence on neural substrates linked to different domains of the self such as high-level self-trait processing and low-level self-face recognition in an implicit and automatic fashion. Research along this line has stimulated the emergence of cultural neuroscience (Chiao and Ambady, 2007; Han and Northoff, 2008).

In this paper, we first review neuroimaging findings regarding the neural substrates underlying different domains of the self. We then present recent transcultural neuroimaging studies that have shown preliminary evidence for cultural influences on neural mechanisms of self-related processing. We finally discuss how the neuroimaging observations help us to conceptualize the self in psychological and philosophical terms.

Neural correlates of self-related processing

Neuroanatomy of self-relatedness and social processing

The last decade has witnessed an increasing number of functional neuroimaging studies focusing on self-related processing or self-referential processing (Phan et al., 2004; Craik et al., 1999; Kelley et al., 2002; Turk et al., 2003; Northoff and Bermpohl, 2004). A recent meta-analysis of imaging studies on the self demonstrated an involvement of medial cortical regions in self-related tasks across different domains (motor, emotional, memory, verbal, spatial, facial, and social) (see Northoff et al., 2006). Results from neuroimaging studies indicate that the more anterior medial prefrontal cortex (MPFC) is implicated in the self function and consists of Brodmann areas (BAs) 9 and 10 (medial regions), 24, 25, and 32, with 11 and 14 in the medial orbital cortex. In addition, the more posterior (caudal) regions are also involved in the self function, specifically the posterior cingulated (PCC), precuneus, and retrosplenial regions. The more anterior dorsal regions, in particular the dorsal MPFC (DMPFC), have been activated in many studies on the self, which include a strong evaluative or judgmental component (e.g., Zysset et al., 2002; Johnson et al., 2002), while the more rostral, ventral regions have been activated in studies that had a self-reflection component (e.g., Seger et al., 2004; Kelley et al., 2002; Lieberman et al., 2004). Finally, the more posterior central midline structures have typically been activated in tasks involving autobiographical memory (e.g., Fink et al., 1996; Piefke et al., 2003). The relationship between the anterior and posterior CMS has also been investigated in a recent PET–TMS study (Lou et al., 2004). Analysis of functional connectivity revealed a significant interaction between the DMPFC, the posterior cingulated, precuneus, as well as other regions (lateral prefrontal, inferior parietal, and middle temporal).

In parallel to the impressive development in the functional neuroanatomy of self-related processing, neuroimaging studies of the processing of social stimuli also developed extensively. The cognitive and emotional processes involved in response to social stimuli have been coined "social cognition," which includes (among others) knowledge about the self, perceptions of others, and interpersonal motivations. More recently, investigation of the functional neuroanatomy of social cognition has become one of the main streams in social psychology and gave birth to a new interdisciplinary field of social cognitive neuroscience (Ochsner and Lieberman, 2001). The central premise here is that dedicated brain systems have developed to process social stimuli, parallel to the dedicated neurophysiological processes underlying inherently social behaviors such as grooming and cooperation (e.g., Caldji et al., 1998; Rilling et al., 2002). In neuroimaging studies, social cognition has recently been associated with activity in brain regions, such as the MPFC and the anterior cingulate cortex (ACC), the temporo-parietal junction, the superior temporal sulcus, and the temporal poles (Amodio and Frith, 2006).

Converging findings implicate MPFC involvement in both social cognition and self-related processing and provide strong empirical support to our view presented above. If social salience is processed by the MPFC and reflects the relation between others and oneself, the MPFC should be activated by the processing of oneself and others. This has indeed been the case; MPFC structures have been activated when subjects formed impressions about people as opposed to objects (Mitchell et al., 2005a, b) or observed social interactions between others (Iacoboni et al., 2004; Han et al., 2005). The neuroanatomical convergence of self-relatedness and social cognition is not limited to the MPFC, but can be seen in additional brain regions that have been associated with social cognition and with the self function, like the PCC. The PCC activates with social as compared to more visceral emotions (Britton et al., 2006), but also with self-generated emotions (Damasio et al., 2000), in response to listening to autobiographical scripts (Fink et al., 1996). In addition, studies that have investigated self-referential processing through autobiographical memory (Cabeza et al., 2004), self-association tasks (Phan et al., 2004), and self-related judgments (Johnson et al., 2002; Kelley et al., 2002) have also implicated both the PCC and MPFC. The differential role of rostral versus caudal structures, in determining self-relatedness, remains to be established.

"Self" and "other"

Our conceptualization of self-relatedness offers a different perspective on the question of "self" versus "other." Traditionally, "self" and "other" were viewed as distinct categories and thus often contrasted in functional neuroimaging research. We however propose that the "other" person is perceived, by the self-relatedness function, on a continuum from self to nonself. Here, the "self" is the extreme end of a spectrum of self-relatedness, and the "other" is on the same continuum but not to the same degree. It is likely tagged as "like-self but not-self," and thus these two concepts are "tagged" by the same brain regions. The ability to identify conspecifics as "like-self but not-self" allows the organism to define relative relatedness of group members, predict behaviors, develop empathy, share resources, and navigate in complex social environments. In fact, this ability to create an internal "map" of self-relatedness likely offered a selective advantage during evolution, particularly for species with complex social organizations, and thus became highly complex and evolved in humans.

Imaging studies indeed report an overlap between the processing of the self and others, especially in the DMPFC and ventral MPFC (VMPFC) (Schmitz et al., 2004; Platek et al., 2004; Seger et al., 2004; Beer et al., 2006). However, neural dissociation between the self and others has been observed within the same regions, as well as in other lateral prefrontal, parietal, and temporal cortical regions (Craig, 2002; Kelley et al., 2002; Platek et al., 2004; Seger et al., 2004; Schmitz et al., 2004; Ochsner et al., 2005). How can one reconcile such discrepancy? The key issue here might be the degree of self-relatedness of the other person; the more the other is identified as self-related, the greater the similarity between VMPFC/DMPFC responses to the self and other. Mitchell et al. (2005a, b) who found that the more the similar subjects rated others' faces to their own, the greater the activation observed in the VMPFC, suggesting that the VMPFC is engaged in viewing others in terms of one's own self, thus providing support to the simulation theory (see also Mitchell et al., 2006). These empirical data support our notion of a common, self-related processing, underlying both self and other on a self–nonself continuum rather than a self–nonself dichotomy. Conceptually, the distinction between the self and other is not primarily relevant to our brains' processing, which instead may represent and code a "more primary intersubjectivity" (see also Iacoboni, 2006) in terms of self-likeness.

Self-related processing as implicit and automatic

We assume that self-related information processing does not typically occur on an explicit and consciously aware level, even though it may be rich in affective consciousness (Panksepp, 2007). Instead, it can be either cognitively preconscious or unconscious and thus implicit, but accompanied by experienced shifts in affective feeling states that are prepropositional and hence hard to put into words.

The concept of an automatic self (Koole et al., 2001) has been suggested and characterized by operating automatically at an implicit, cognitively nonreflective level, yielding automaticity in self-evaluation without deliberative thought, often in situations with decreased cognitive control, and commonly associated with positive emotions. Lieberman et al. (2004) further proposed an X-system for the processing of intuition-based implicit and automatic self-knowledge and a C-system for the processing of evidence-based, nonautomatic, conscious self-knowledge. They also showed evidence that the X-system is associated with the VMPFC, nucleus accumbens, and amygdala whereas the C-system is linked to the lateral prefrontal cortex, hippocampus, and posterior parietal cortex.

How are the ‘‘implicit and affective forms of selfhood’’ (we assume these are the nomothetic aspects of the self) and the various ‘‘explicit and cognitive forms of selfhood’’ (the idiographic aspects) related to each other in neurobiological terms? Some studies reported activation (and increased functional connectivity) in anterior and posterior CMS during self-related tasks with low cognitive load (Kjaer et al., 2002; Lou et al., 2004). Conversely, deactivation (and low functional connectivity) in CMS has been observed in tasks with high cognitive load and low degrees of self-relatedness (Gusnard et al., 2001; Kelley et al., 2002). The implicit and explicit aspect of self-related processing may be integrated through the interaction between subcortical and cortical midline regions (Panksepp and Northoff, 2009). Subcortical regions may determine the basic self-relatedness of the organism by coding the relation between different stimuli: interoceptive, exteroceptive, motor, and emotional. This relation is expressed in affective and valuative terms. The resulting ‘‘sense of relatedness’’ may then be further elaborated in cortical midline regions in cognitive and temporal terms. Higher-order cognitive abilities like attention, impulse control, working memory, executive functions, etc., may allow a representation of the ‘‘sense of relatedness’’ on a cognitive or high mental level independent of any actual stimulus. This allows an organism to distinguish one’s ‘‘sense of relatedness’’ from others’ ‘‘sense of relatedness’’ and thus from the environment, resulting in what we above called the ‘‘sense of distinction.’’

Cortical midline regions may also regulate the subcortically established ‘‘sense of relatedness’’ temporally. Recent studies in humans indicate that the CMS are involved in both anticipating future events and recollecting past events (Schacter and Addis, 2007). Furthermore, self-relatedness induced delayed signal changes more in CMS than in subcortical structures (Schneidera et al., 2008). Thus, it is likely that CMS may be crucially involved in temporally extending the subcortically processed here-and-now immediacy of self-relatedness. By delaying or anticipating neural activity and dissociating it from the presence of the actual stimulus, CMS may put the already established self-relatedness into a wider temporal context when compared to subcortical regions where it seems to be tied to the actual presence of internal or external stimuli and state-control functions (e.g., basic homeostatic and emotional states).

Cultural influence on neural substrates of self-related processing

Cultural difference in self-referential processing: overlap between the self and close others

Unlike the Western philosophy that often discusses the unique dispositions to define the self or self–other distinctions, East Asian philosophy puts strong emphasis on human connections with each other in social contexts and believes that the highest achievement of a person is the identification of the individual with the universe (Zhu and Han, 2008). The difference in philosophical thinking of the self has influenced greatly the formation of psychological concept of the self. For instance, the Western cultures result in an independent view of the self with a bounded structure that emphasizes unique dispositions or traits of the self that keep invariant across different social contexts, whereas the East Asian cultures produce an interdependent view of the self with a variable structure that stresses the fundamental connections between the self and others and between the self and social contexts (Markus and Kitayama, 1991). Does such cultural influence extend to the neural substrates underlying the processing of self-related information?

To address this issue, we (Zhu et al., 2007) scanned two cultural groups (i.e., English-speaking Westerners and monolingual Chinese subjects) while they performed trait judgment tasks regarding self and a close other (i.e., mother). Cultural universal neural activity related to the self-referential processing was localized to the MPFC and the anterior ACC by contrasting trait judgment of the self and trait judgment of a public person in both cultural groups. An interesting finding of this work is that, relative to trait judgment of the public person, trait judgment of one's mother also activated the MPFC in Chinese subjects, providing evidence for shared neural structure for representation of both the self and a close other. However, Western subjects did not show increased activation in any brain areas in the contrast of mother-judgment compared to other-judgment. The findings provide the first piece of neuroimaging evidence for cultural difference in the neural structure of the self. Specifically, Chinese individuals use the MPFC to represent both the self and the mother whereas Westerners use the MPFC to represent exclusively the self. Zhu et al.'s (2007) work contrasts with Heatherton et al.'s (2006) observation that MPFC activity failed to differentiate between the self and a close other (i.e., the best friend) in North Americans. However, as there has been no research that compared Chinese self and the best friend, it is unknown whether the neural structure of the Chinese self extends to the degree to include other close persons besides mother.

Cultural values differ between two cultural groups as well as among individuals in a specific cultural group. For example, in one cultural group, some individuals show greater extent of adherence to individualism and independent self whereas others show greater extent of adherence to collectivism and interdependent self (Chiu and Hong, 2006). Can the magnitude of neural activity in the brain area related to self-referential processing predict individuals' difference in self-construal styles? Chiao et al. (2009) recently scanned Caucasian Americans and Japanese in tasks requiring judgments of general trait descriptions or contextual self descriptions. Moreover, they assessed individuals' degree of endorsement of independent and interdependent self-construals using Self-Construal Scale (Singelis, 1994). While Chiao et al. did not observe significant interaction between cultural groups and different judgment tasks in modulation of MPFC activity, they found positive correlation between MPFC activity differentiating contextual and general trait judgments and the degree of interdependent self-construal style. The results provide further evidence for the influence of cultural values on individuals' neural substrates underlying self-reflective thinking.

While these neuroimaging studies suggest that Western/East Asian cultures result in variation of the contents of the self and the underlying neural activity, other cultural beliefs may strongly modulate the way of thinking of the self. For example, Christianity advocates denial of self or self-transcendence in order to highlight human contingency and dependence on God (Burns, 2003; Ching, 1984). Moreover, Christianity emphasizes judgment of the self from God's perspective rather than from one's own perspective. Since the VMPFC plays a key role in coding self-relatedness of stimuli (Moran et al., 2006; Northoff et al., 2006), Han et al. (2008) predicted that Christian beliefs weaken the process of coding self-relatedness of stimuli and thus induce decreased activity in VMPFC. In addition, taking others' perspective during self-judgment may activate the brain area that is involved in theory-of-mind such as DMPFC. To test these hypotheses, Han et al. (2008) scanned both Chinese nonreligious and Christian subjects in trait judgment tasks associated with self and others. The Christian subjects had been attached to the local faith communities for 1–7 years when participated in the study. While the fMRI results from nonreligious subjects replicated previous findings by showing increased activation in VMPFC during self-judgment relative to other-judgment, a different pattern of the brain imaging results was observed in Christian subjects. Both ROI and random effect analyses did not show significant activation in the VMPFC when Christian subjects made judgment regarding the self as compared to others. However, there was evidence that the DMPFC activity increased when Christian subjects made trait judgment about the self relative to others. Using bootstrap analysis, Han et al. demonstrated that the distinct pattern of MPFC activity in association with trait judgment of the self (i.e., decreased activity in the VMPFC but increased activity in the DMPFC) can be used to classify the two subject groups well. Since the VMPFC and DMPFC are, respectively, involved in the representation of stimulus self-relevance and the evaluation of self-referential stimuli (Northoff et al., 2006), the findings suggest that adopting Christian beliefs may result in weakened neural encoding of stimulus self-relatedness but may enhance neural activity in areas that mediate the evaluative process applied to self-referential stimuli.

Cultural difference in neurocognitive processing of self-recognition: implicit and automatic processing of the self

Another important aspect of self-processing is self-face recognition, that is, to recognize oneself in a mirror, which has been proposed to reflect the ability to become the object of one's own attention (Gallup, 1970) and to be an indicator of high-level self-awareness (Keenan et al., 2000). A number of neuroimaging studies have investigated the cortical underpinnings of self-recognition by comparing neural activity in association with one's own face and faces of other individuals. The accumulating evidence suggests that a distributed network consisting of the fusiform gyrus, middle and inferior frontal gyrus, and precuneus is involved in self-face recognition when compared with recognition of faces of other individuals (Platek et al., 2008). While both Westerners and East Asians were recruited in the previous research of self-recognition, there has been no research exploring potential cultural difference in neural mechanism underlying self-recognition. However, given the Western/East Asian cultural difference in self-construal styles (Markus and Kitayama, 1991) and the consequent cultural modulation of neural substrates of self-referential processing (Zhu et al., 2007; Chiao et al., 2009), one would expect similar cultural influence on the neural mechanisms of self-recognition. Specifically, the Western independent self may assign greater social salience or positive association with one's own face than to others' faces (Ma and Han, in press), which in turn results in stronger attention to one's own face when presented among others' faces and induce deeper processing of the own-face. In contrast, as the East Asian interdependent self emphasizes social connections between the self and others, enhanced processing of one's own face may not be as strong as that in Westerners.

To test this hypothesis, we (Sui et al., 2009) recently recorded event-related potentials from British and Chinese subjects while they judged head orientations of their own face or a familiar face in visual displays. We first observed faster responses to one's own face relative to the familiar face in both cultural groups. However, the self-advantage in behavioral performances was greater for British than for Chinese subjects, suggesting that the own-face captures attention to a larger degree in the British than in Chinese. More interestingly, the pattern of the ERP results showed a reverse pattern in the two cultural groups. We found that one's own face elicited a larger negative activity at 280–340 ms over the frontal–central area (N2) relative to the familiar face in the British. In contrast, the Chinese showed weakened self-advantage in behavioral responses and reduced anterior N2 amplitude to the own-face compared with the familiar face. The frontal–central N2 component is sensitive to perceptual salience of stimuli (Folstein and Petten, 2008). The N2 is also involved in differentiation between different facial expressions (Kubota and Ito, 2007) and between faces of different races (Ito and Urland, 2003), suggesting that the N2 is associated with deeper processing of faces to benefit individuating. Thus, the reverse pattern of the N2 results in the cultural groups suggests that the independent self-construals endow the own-face with higher social significance relative to familiar faces whereas the interdependent self-construals may assign higher salience to familiar faces.

To further explore the potential cause–effect relation between self-construals and self-recognition, we (Sui and Han, 2007) scanned Chinese subjects while they performed an implicit face recognition task that required judgments of orientations of one' own face or a familiar face. The contrast between the two judgment tasks revealed the effect of implicit recognition of the own face. However, subjects were primed before the face recognition task with either independent or interdependent construals (Gardner et al., 1999) by marking independent (e.g., I, mine) or interdependent (e.g., we, ours) pronouns in an essay. We found that the neural activity in the right middle frontal cortex increased to the self-face than familiar faces. In addition, the right frontal activity differentiating between the self and familiar faces was enlarged by the independent relative to interdependent self-construal priming. The increased right frontal activity was associated with faster responses to self than familiar faces. The findings suggest that shifts of self-construal styles induced modulation of neural underpinnings of self-face recognition that is supposed to reflect self-awareness and thus provide preliminary evidence for the interplay between self-construals and the neural substrates underlying self-face recognition. The findings support the view that the influence of cultural differences on self-concept may extend beyond the processing of personal trait and modify the neural mechanism underlying the processing of the physical self (e.g., face). As mentioned above, the CMS plays a pivotal role in self-processing. A challenge for future research is to uncover the way the neural activity in the CMS interacts with the activity in other cortical areas in a specific sociocultural context and thus results in cultural specific neural underpinnings of cognitive processes.

Conclusion

Recent neuroimaging studies have shown strong evidence that humans evolve neural mechanisms mediating self-related processing that encode the strength of stimulus's relation to the self and to environmental contexts. In addition, as the strength of the self-stimulus relation emerges gradually through learning during development, the neural substrates underlying self-referential processing are strongly influenced by sociocultural contexts. Culture-specific neural mechanisms afford unique self-concepts or self-construal styles that help individuals to adapt to the accompanying cultural and social environments so that individuals can function efficiently during social interactions. The transcultural neuroimaging findings of culturally distinct neural representations of the self help to understand the nature of self-construals and the social significance of self-related stimuli and their implicit and automatic processing. The findings also assist in understanding how others in different cultures are represented in terms of the relation to the self, indicating that the self–other relationship is highly flexible in its neural manifestation and dependent on the social context.

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CHAPTER 15

Cultural effects on the neural basis of theory of mind

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Abstract: "Theory of mind" has been described as the ability to attribute and understand other people's desires and intentions as distinct from one's own. It has been found to develop as early as between 3 and 4 years old, with precursor abilities possibly developing much earlier. There has been debate about the extent to which the developmental trajectory of theory of mind may differ across cultures or language systems. Although very few neuroimaging studies have directly compared different groups from different culture and language systems, across studies of a number of cultural/language groups have been used to explore the neural correlates of theory of mind. A summary of these findings suggests that there may be both universal and culture or language-specific neural correlates related to theory of mind. These studies, while still preliminary in many ways, illustrate the importance of taking into account the cultural background of participants. Furthermore these results suggest that there may be important cultural influence on theory of mind and the neural correlates associated with this ability.

Keywords: theory of mind; culture; social cognition; fMRI; medial prefrontal; temporoparietal junction

Introduction

Theory of mind has been defined as the ability to impute mental states to both ones self and others (Premack and Woodruff, 1978; Wimmer and Perner, 1983). Since the first test of theory of mind in a chimpanzee (Premack and Woodruff, 1978), a number of paradigms have been devised to test theory of mind in humans (Baron-Cohen, 2000). Among those tasks, false-belief tasks have been among the most widely used both for testing normally developing (Wimmer and Perner, 1983) as well as atypical pediatric populations (Baron-Cohen et al., 1985; Baron-Cohen, 2000).

False-belief tasks come in a variety of versions but all involve a protagonist who has some false belief and a subject who has actually knows the true facts of the situation. One of the most common has been termed the "unexpected location" task (Baron-Cohen et al., 1985, 1986). In this task, a protagonist sees an object being placed in a certain location. The protagonist then leaves and the object is moved. When the protagonist returns, he or she mistakenly believes the object is still in its initial location. The question to the subject is where the protagonist thinks the object is located. The key concept to be demonstrated is that the subject understands that the protagonist has a false belief about the location. False-belief tasks like this have been used as a litmus test to determine if a person has developed a theory of mind (Happé and Loth, 2002).

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After many variations of these tasks, a general pattern of results has emerged. Four-year-old children are generally able to succeed at false-belief tasks, whereas 3-year-old children tend to fail. In addition, older children or adolescents with autistic spectrum disorders often perform poorly (Baron-Cohen, 2000). This pattern has been hypothesized to be universal regardless of culture (Wellman, 1998). However, a recent meta-analysis comparing non-Western (China and Hong Kong) and North American (United States and Canada) children found similar development trajectories but wide variations in developmental timing across cultures (Liu et al., 2008). For example, the onset of false-belief understanding in Canadian children appeared around 3 years of age, whereas Hong Kong children showed similar performance as much as 2 years later (Liu et al., 2008). These results suggest both universal influences on theory of mind development as well as effects of experience. In addition, Liu et al's study highlights the importance of including non-Western cultures when exploring possible cultural effects on the development of any concept or process.

Over the last, almost, 15 years, a number of studies have explored the possible neural correlates of theory of mind. Many of these studies have worked to understand possible universal neural correlates of theory of mind (e.g., Gallagher et al., 2000; Frith and Frith, 2001, 2003). However, as indicated by this volume, recently researchers have begun to shift their attention to the possible cultural variations in the neural underpinnings of various social cognitive functions including theory of mind. In this article, we explore three primary topics in this ongoing effort. These include (1) the findings of cultural and cross-cultural behavioral studies of theory of mind; (2) results of neuroimaging studies of theory of mind and related socio-cognitive functions; (3) implications, limitations, and future directions of these results.

Behavioral explorations of cultural variation in theory of mind development

There has been debate about the extent to which the developmental timing and trajectory of theory of mind ability depends on culture and language. Some of the cross-cultural studies have supported the universal developmental pattern of theory of mind (Avis and Harris, 1991; Naito et al., 1994; Lee et al., 1999; Tardiff and Wellman, 2000; Callaghan et al., 2005; Yazdi et al., 2006), whereas others have found differences in non-Anglo children compared to European/American children (delays in non-Anglo children: Chen and Lin, 1994; Wahi and Johri, 1994; Vinden, 1999; Koyasu, 1997; Louis, 1998; Goushiki, 1999; Naito, 2003; Naito and Koyama, 2006; Liu et al., 2008 and advancements in non-Anglo children: Shatz et al., 2003). For example, Callaghan et al. (2005) found that local children in Canadian, Indian, Peru, Samoa, and Thailand all pass the false-belief task at about the same time. They concluded that onset of false-belief understanding is tightly synchronous across different cultures. However, other studies show dramatically different onsets, with fewer than 60% of Japanese 5–6-year olds passing the standard false-belief task (e.g., Koyasu, 1997; Goushiki, 1999; Naito, 2003). Moreover, the results that seem to show no difference across culture/language do not necessarily rule out that there may be cultural/linguistic influence on "how" theory of mind is understood. The forced-choice style false-belief tasks used in the majority of the cross-cultural studies make it difficult to detect strategic differences. For instance, in a study with Mandarin-speaking children, Chinese children's performance for the false-belief task was comparable to Western children's performance. However, their performance was influenced by the choice of verb (i.e., three verbs that all mean "think") used in the false-belief task (Lee et al., 1999). These results indicate possible strategic differences influenced by linguistic variations.

Compared to possible differences due to linguistic variation, those due to cultural variation can be difficult to detect because it is harder to specify exactly what cultural variables may affect theory of mind performance. Vinden (1999) examined emotional false-belief understanding in children from Papua New Guinea, Africa, and Western-influenced countries. While all children came to understand emotion based on desire, only

Western culture children came to understand emotion based on belief by 6 years of age. These results may indicate that at least these non-Western children progress differently in the development of their emotion understanding and the relationship between emotion and internal states of minds.

Similarly, Naito and Koyama (2006) found a striking delay in false-belief understanding in Japanese children (as much as 2 years delayed from Western children). Moreover, even when answering correctly, the justifications the Japanese children gave differed from those typically given by Western children. Most Japanese children referred to behavior (e.g., "she was there first") or social rules (e.g., "he said to wait there"), rather than the internal and personal justifications (e.g., "he wanted the toy") commonly given by children from Western cultures (e.g., Bartsch and Wellman, 1989; Wimmer and Mayringer, 1998). These types of results suggest that children across cultures may understand theory of mind in different ways. While Western children may conceptualize theory of mind as being personal and intentional, at least some non-Western cultures may conceptualize theory of mind as being mostly situational and interpersonal.

Brain imaging explorations of neural correlates of theory of mind

To date, a number of brain imaging studies have examined the neural correlates of theory of mind using a variety of paradigms (Fletcher et al., 1995; Goel et al., 1995; Happé et al., 1996; Brunet et al., 2000, 2003; Gallagher et al., 2000; Vogeley et al., 2001; Ferstl and von Cramon, 2002; Saxe and Kanwisher, 2003; Walter et al., 2004; Kobayashi et al., 2006, 2007a, b, 2008; Saxe and Powell, 2006; Sommer et al., 2007; Abraham et al., 2008; Lissek et al., 2008). Many of these studies have found significant activity in the medial prefrontal cortex (mPFC) or anterior cingulate cortex (ACC) during false-belief conditions (e.g., Fletcher et al., 1995; Goel et al., 1995; Happé et al., 1996; Brunet et al., 2000, 2003; Ferstl and von Cramon, 2002; Kobayashi et al., 2006, 2007b, 2008). Additionally, the temporoparietal junction (TPJ) has also been found to be important for theory of mind processing (Saxe and Kanwisher, 2003; Saxe and Powell, 2006). Other brain areas that have sometimes been shown to be involved in theory of mind tasks include dorsolateral prefrontal cortex (DLPFC), precuneus/posterior cingulate cortex (PCC), superior temporal sulcus (STS), and temporal pole (TP).

Although rarely mentioned in the synthesis of the above work, the studies completed thus far have used participants from a few different cultural and/or linguistic backgrounds (though often from Western cultures). In their seminal study using positron emission tomography (PET), Happé et al. (1996) examined the neural basis of theory of mind in Swedish adults with and without Asperger syndrome. They found greater activity in the mPFC in the typically developed control group compared to the Asperger group (Fig. 1). Brunet et al. (2000, 2003) tested French adults with comic strips depicting intentional and non-intentional (control) stories and found more brain activity in several regions including the mPFC during intentional processing. A number of studies have tested German adults with various theory of mind paradigms and implicated several areas including the mPFC and STS (Vogeley et al., 2001; Ferstl and von Cramon, 2002; Walter et al., 2004; Sommer et al., 2007; Abraham et al., 2008; Lissek et al., 2008). Our examinations of adults and children with non-Western background using a false-belief paradigm have shown theory of mind sensitive activity in the mPFC (among other regions) (Kobayashi et al., 2006, 2007a, b, 2008).

Putative neural correlates of theory of mind: universal or culture dependent?

The studies discussed above suggest neural correlates of theory of mind that are possibly both culture dependent and culture independent. In what follows, we discuss some of the brain regions implicated in the literature, in terms of their putative roles in processing either universal or culture/language-specific aspects of theory of mind.

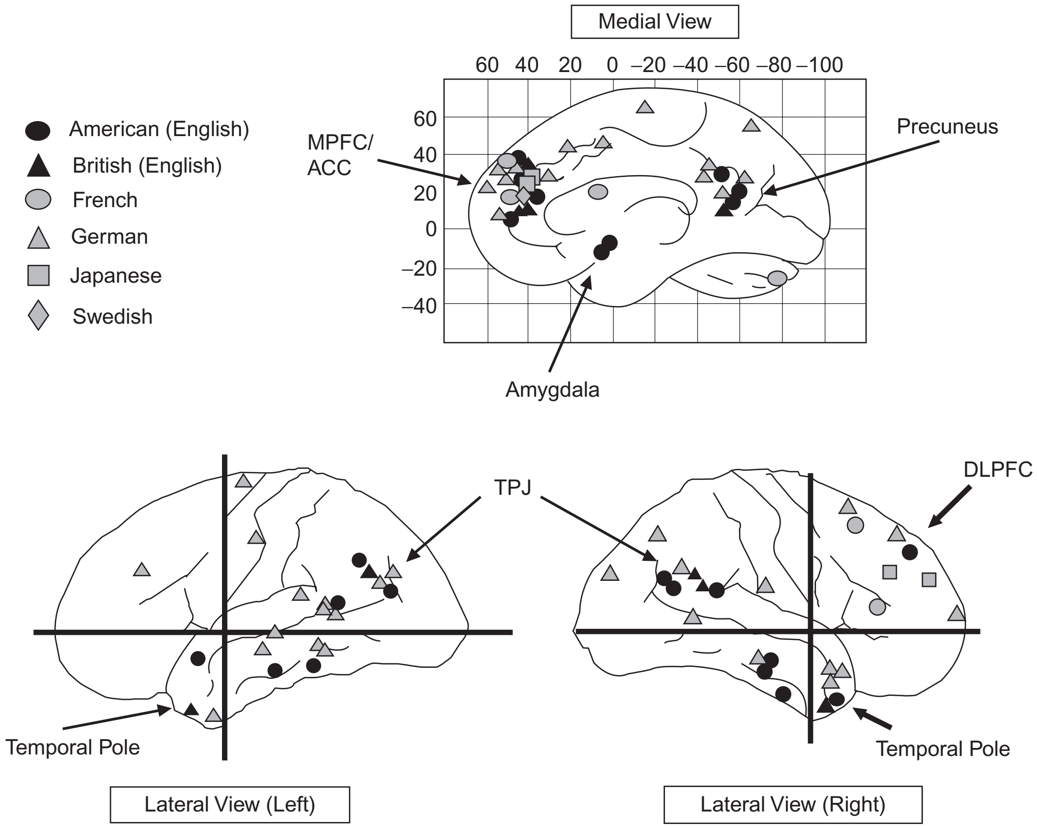

Fig. 1. Brain diagrams showing the brain regions implicated in selected theory of mind neuroimaging studies that used false-belief style paradigms. Montreal Neurological Institute (MNI) coordinates were converted to Talairach coordinates (Talairach and Tournoux, 1988) (http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml). Selected studies are as follows. *American*: Goel et al. (1995), Kobayashi et al. (2006), Saxe and Kanwisher (2003), Saxe and Powell (2006). *British*: Fletcher et al. (1995), Gallagher et al. (2000). *French*: Brunet et al. (2000, 2003). *German*: Abraham et al. (2008), Ferstl and von Cramon (2002), Lissek et al. (2008), Sommer et al. (2007), Vogeley et al. (2001), Walter et al. (2004). *Japanese*: Kobayashi et al. (2006). *Swedish*: Happé et al. (1996).

Medial prefrontal cortex and anterior cingulate cortex

The ACC/mPFC has been one of the most consistently implicated region using a variety of theory of mind tasks across a number of cultures (Fig. 1). The mPFC has been suggested to be involved in a self-referential component of theory of mind (Ochsner et al., 2004; Mitchell et al., 2005). According to one review, the mPFC may be further divided into functional subregions: the posterior rostral mPFC, the anterior rostral mPFC, and the orbital mPFC involving cognitive, emotional, and rewarding aspect of theory of mind, respectively (Amodio and Frith, 2006). The ACC has also been conceptualized as potentially divisible into cognitive (dorsal ACC) and emotional (ventral ACC) subregions (Bush et al., 2000). Among these regions, the anterior rostral mPFC (together with a part of ventral ACC) seems to be the one that is most consistently recruited for different theory of mind tasks across cultures (Fig. 1). Thus, we hypothesize that the anterior rostral mPFC and ventral ACC may be involved in theory of mind processing, specifically the emotional and self-related aspects, regardless of culture. There is debate, however, about the role of mPFC in theory of mind. Two studies with patients with frontal damage have found intact theory of mind performance (Fine et al., 2001;

Bird et al., 2004). Saxe (2006) had argued that although the mPFC is involved in reasoning about mental states, it is related more to the understanding of relationships — the emotional aspects of relationships such as empathy in ventral prefrontal areas and the collaborative aspects in dorsal regions. Clearly, more research across different tasks, cultures, and age groups need to be done to clarify these theories.

Temporoparietal junction

While the majority of the earlier neuroimaging studies of theory of mind implicated the mPFC as the core region for theory of mind (e.g., Fletcher et al., 1995; Goel et al., 1995; Happé et al., 1996; Gallagher et al., 2000; Vogeley et al., 2001), several later fMRI studies found more robust brain activity in the TPJ than in the mPFC (Saxe and Kanwisher, 2003; Saxe and Powell, 2006). In addition, disrupted theory of mind performance has been shown in TPJ-damaged patients (Apperly et al., 2004; Samson et al., 2007). Saxe (2006) has argued that the TPJ is crucial for representing mental states and theory of mind. However, the specialized involvement of the TPJ in theory of mind has been questioned in studies that have found activity in the TPJ while subjects reoriented their attention to any novel stimuli (Corbetta et al., 2008; Mitchell, 2008).

The generalization of TPJ's importance in theory of mind across cultures is still uncertain. TPJ activity specific to theory of mind has not consistently been found across cultures other than American and British adults (see Fig. 1). We did not find theory of mind specific TPJ activity (at $p < 0.05$, uncorrected) in Japanese children and found significantly less theory of mind TPJ activity in Japanese adults (compared to American adults) (Kobayashi et al., 2006; Kobayashi et al., 2007b; see also Perner and Aichhorn, 2008).

One possibility is that potential cultural differences in TPJ activity in theory of mind tasks are due to different cultural approaches to theory of mind. Some research has suggested that the TPJ may be involved in distinguishing self-agency from other agency (Blakemore and Frith, 2003; Jackson and Decety, 2004; Decety and Grézes, 2006). If one culture had a more self–other distinction of theory of mind, perhaps the TPJ would be more involved in their processing.

Some studies have suggested that Japanese culture may encourage intersubjective or situational *mentalizing* over a subjective approach (Naito, 2007; Naito and Koyama, 2006). While Indo-European language speakers may conceive of an event based on the action-agent model (Werner and Kaplan, 1963), Japanese speakers may tend to frame the event as a situation that is beyond the agent's control (Maynard, 1997). One hypothesis therefore is that the diminished activity in TPJ in Japanese children and adults (Kobayashi, 2006, 2007b) might reflect the reduced sense of self–other distinction in the Japanese culture.

There may be variability in this type of interdependent versus independent thought even in Western cultures. A large-scale comparative study involving more than 5000 participants from 29 nations (including Asian, European, and North American nationals) indicated that interdependency is correlated with low English-language fluency (Fernández et al., 2005). In addition, it has been demonstrated that, unlike Anglo-Americans, 3–5-year-old French children rarely use the subjective ''belief'' concept to justify the behaviors in false-belief task (Bradmetz, 1998). It is not clear why several neuroimaging studies of theory of mind conducted in continental European countries (French, Swedish, and several German) did not find the theory of mind specific activity in the TPJ. One hypothesis, that clearly needs more explicit testing, is that at least individuals from continental European cultures may also conceptualize theory of mind in less self-referential way. We believe that more work in different cultures needs to be done to determine whether TPJ theory of mind specific activity is truly culture independent or whether it is especially engaged in Anglo-American cultures.

Other putative theory of mind regions (PCC/Precuneus, DLPFC, and TP)

The PCC or precuneus area has been among the most frequently implicated regions in the theory of mind neuroimaging studies. Given that not only American/British (Fletcher et al., 1995; Gallagher et al., 2000; Saxe and Powell, 2006) but also German (Ferstl and von Cramon, 2002; Vogeley et al., 2001; Walter et al., 2004; Sommer et al., 2007) and Japanese (Kobayashi et al., 2006) adults showed activity in this area for theory of mind (vs. a variety of non-ToM conditions), the PCC's involvement in theory of mind may also be culture independent. Vogeley and Fink (2003) suggest that the PCC or medial parietal cortex is important for the formation of first person perspective. Moreover, along with the mPFC, this region has been hypothesized to be active during a default mode or baseline condition when subjects may be self-ruminating (Gusnard and Raichle, 2001; Gusnard et al., 2001; den Ouden et al., 2005). Perhaps, the precuneus/PCC is involved in processing some first person-related intentional aspects of theory of mind or the self-ruminating aspects of the default network in a culture-independent manner.

The DLPFC has been implicated as being important for executive function (e.g., Frith and Dolan, 1996; MacDonald et al., 2000). DLPFC activity may be related to inhibitory control involved in theory of mind (Saxe et al., 2004; Kain and Perner, 2005). For instance, in the false-belief scenario, one has to inhibit the first (or second in the case of the second-order false-belief task) character's belief or thought. At least five brain imaging studies that tested French (Brunet et al., 2000), German (Vogeley et al., 2001; Sommer et al., 2007), British (Gallagher et al., 2000), and Japanese and American adults (Kobayashi et al., 2006) have found activity in this area for cartoon or story-based theory of mind. It is possible that involvement of DLPFC is related to inhibitory control in certain theory of mind tasks but in a culture-independent manner.

Several theory of mind imaging studies across cultures found activity in the anterior tip of STS or TP (Gallagher et al., 2000; Vogeley et al., 2001; den Ouden et al., 2005; Abraham et al., 2008). However, we found significant difference between American and Japanese groups in this area (Kobayashi, 2007). In our study, American adults and children had more activity in this area than the Japanese adults and children during the same cartoon theory of mind task. Therefore, theory of mind activity in the TP (especially the right TP) may be culture dependent.

The TP have been implicated in a number of related operations. TP regions are activated when one retrieves autobiographical or episodic memory (Fink et al., 1996; Maguire and Mummery, 1999; Maguire et al., 2000). Frith and Frith (2003) have suggested that this area may be responsible for accessing social knowledge in the form of scripts, which aid interpretation of social situations. In Naito's 2003 study on Japanese children's theory of mind, she not only found a delay in theory of mind, but also a correlation between the children's theory of mind and performance in self-related episodic memory. One possibility, again that needs confirmation, is that people from Japanese culture recruit the TP to a lesser magnitude than Americans during theory of mind processing because their access to episodic memory is more automatic than Americans.

Limitations and future directions in cultural neuroimaging studies of theory of mind

There are several limitations of the current cross-cultural research (both behavioral and neuroimaging) of theory of mind that need to be considered. One clear limitation is the paucity of cross-cultural neuroimaging research of theory of mind overall. Even though there are a number of within cultural brain imaging studies of theory of mind, so far, ours are the only cross-cultural studies that have tried to compare neural correlates of theory of mind between the two cultures: Japanese and American (Kobayashi et al., 2006, 2007b, 2008). However, ours is not a true cross-cultural study, since the Japanese subjects were bilingual and lived in the United States at the time of the experiment. Ideally, as in behavioral studies, cross-cultural variation should be tested against clearly defined within cultural variation. Cross-cultural theory of mind brain imaging studies that compare subjects from two (or more) distinct cultures need to be completed to gain a more thorough understanding.

Another clear limitation of cross-cultural theory of mind research overall (see Vinden, 1999 and Lillard, 1998a, b) is that the standard false-belief task may not be valid for all cultures. Many non-Western cultures do not construe behaviors as personal and intentional. Results of Naito and Koyama (2006) have shown that many Japanese children rarely give desire-based explanation to account for the false belief of the protagonist. These results (together with Vinden's, 1999, results) call into question the applicability of the developmental order of theory of mind concepts — from desire-based understanding to belief-based understanding (Wellman and Liu, 2004) — to all cultures. As we mentioned earlier, the forced-choice false-belief task may not measure these qualitative differences in theory of mind understanding. Future cross-cultural brain imaging studies of theory of mind might target some clearly defined cultural variables (e.g., subjectivity vs. intersubjectivity) that might account for strategic differences in false-belief understanding.

Another major limitation is the scarcity of developmental neuroimaging research of theory of mind. Brain imaging studies of theory of mind related tasks in children are relatively few (Ohnish et al., 2004; Dapretto et al., 2006; Wang et al., 2006a, b; Kobayashi et al., 2007a, b). We found some cross-cultural differences in the neural basis of theory of mind in Japanese and American children (Kobayashi et al., 2007b) although they were much smaller than the differences found in adults (Kobayashi et al., 2006). Nativistic theories of theory of mind suggest that at least core set of mental concepts are resistant to cultural variation throughout development (Bruner, 1990; Wellman, 1990). They also presume that these core sets have clearly defined neural basis (Gallagher et al., 2000; Leslie, 2005; and see Barrett and Kurzban, 2006, for a different view that does allow cross-cultural variation in neural basis of theory of mind). In fact, our study found several brain regions that showed convergent activity across cultural and age groups (Kobayashi, 2007). Thus, more neuroimaging studies in children across different cultures are called for to examine whether or not these brain regions subserve the universal core sets of theory of mind.

Lastly, differences in theory of mind related brain activity across cultures could also be attributed to linguistic differences. Although the extent to which language affects neural basis of theory of mind is still debated (Siegal and Varley, 2002), increasing evidence suggests that there may be reciprocal influence between language and theory of mind throughout development (Malle, 2002; Miller, 2006). The processing of pragmatically coherent sentences also recruits the mPFC area (Ferstl and von Cramon, 2002). It may be that the pragmatics or communicative aspects of language profoundly affect theory of mind throughout development, consistent with the finding that people with autism are most impaired in the pragmatic aspects of language (Landa, 2000; Miller, 2006). Since pragmatics is the very aspect of language where cultural constructs often seep in (Fiedler, 2008), it may be difficult to tease apart linguistic effect on theory of mind from cultural one.

Conclusion

Both behavioral and brain imaging research have begun to suggest that some aspects of theory of mind may not be entirely universal. There seem to be differences among cultures in how people understand others' behaviors. These differences may be reflected in at least some variability in the neural correlates of theory of mind across cultures. Several brain regions associated with theory of mind, such as the mPFC, show evidence for possibly being culture independent. Other putative theory of mind regions, such as the TPJ, may be employed by Anglo-Americans, but to a lesser degree by other cultural groups. An important task of future theory of mind research is to define which cultural factors may be affecting theory of mind and examine these factors in systematic ways. These factors may not be only dichotomous (e.g., independence vs. interdependence) but also multifaceted (see Kashima and Kashima, 1997). It may also be problematic to impose a Western assumption of intentionality on false belief to different cultures (see Vinden, 1999).

Many of the theories of theory of mind predict culturally invariant core biological bases of theory of mind at least during early years in life. Thus, an important goal of theory of mind brain imaging research is to explore a possible core neural basis that remains relatively free from cultural influence.

Currently, there are more questions than answers in terms of the neural correlates of theory of mind and how they may vary across development, across languages, and across cultures. However, given some differences have already been suggested in both the brain and behavior of people across different cultures, it seems imperative to at least consider that cultural differences may exist. As all the articles in this volume suggest, studying brain mechanism in one or even two cultures cannot necessarily give you a universal understanding of those processes. Taking culture into account is especially important in processes like theory of mind that may have both cultural and linguistic influences.

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SECTION V

Cultural Neuroscience of Emotion and Well Being

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CHAPTER 16

Culture and social support: neural bases and biological impact

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Abstract: Social support is an effective means by which people cope with stressful events, and consequently, it beneficially affects health and well-being. Yet there are profound cultural differences in the effectiveness of different types of support and how people use their support networks. In this paper, we examine research on the impact of culture on social support, the neural underpinnings of social support, and how cultural differences in social support seeking are manifested biologically. We focus on cultural factors that may affect individuals' decisions to seek or not to seek social support and how culture moderates the impact of support seeking on biological and psychological health outcomes. We also examine recent research on the interaction between genes and culture in social support use. Discussion centers on the importance of developing an overarching framework of social support that integrates health psychology, cultural psychology, social neuroscience, and genetics.

Keywords: culture; social support; emotion regulation; expression

In recent years, researchers have begun to integrate cultural with biological approaches to a wide range of psychological processes (for reviews see Chiao and Ambady, 2007; Han and Northoff, 2008; Levenson et al., 2007). Such integration is important because it enables researchers to understand a phenomenon at both a micro-level, by examining its neural correlates and biological effects, as well as the macro-level, by examining the cultural context within which the psychological process operates. In this spirit, we present research from health psychology, social neuroscience, and cultural psychology that addresses the specific act of social support use.

In this article, we focus on two aspects of the social support process. One aspect involves cultural influences on psychological and biological tendencies that affect individuals' decisions to seek or not to seek social support. Specifically, we discuss cultural divergences in the attention that individuals pay to the social context, in the regulation of emotions, and in the value of expression. The second aspect addresses how culture moderates the impact of support seeking on biological and psychological health outcomes. In particular, we discuss the neural pathways by which social support may modulate stress

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responses and how different types of social support may affect biological stress responses as a function of culture. We also discuss recent research and theorizing on the interaction between culture and genetics in social support use.

Cultural factors affecting the likelihood of seeking social support

Social support exists within the context of relationships, both between individuals as well as between individuals and their respective communities (Cutrona, 1986). Indeed a basic definition of social support emphasizes the embedded nature of individuals within their social context: Social support is information from others that one is loved and cared for, esteemed and valued, and part of a network of communication and mutual obligations (Cohen and Wills, 1985). Thus, all aspects of the support seeking process should be considered within the context of how an individual perceives the role of the self in relationship to others, as well as how people normatively communicate their thoughts and feelings to others; these psychological tendencies vary considerably across cultures (Triandis, 1989; Markus and Kitayama, 1991).

To set the context for this discussion, we focus on the distinction between collectivistic and individualistic cultures and the interpersonal and cognitive differences between them. In individualistic cultures, such as the United States, the dominant model of the self is an independent self that regards a person as possessing a set of self-defining attributes, which are used to take action in the expression of personal beliefs and the achievement of personal goals (Markus and Kitayama, 1991). Relationships also assume an independent form — they are thought to be freely chosen and with relatively few obligations (Adams and Plaut, 2003). Within individualistic cultures, people tend to be analytic in their cognitive style and attend to focal objects more than the context (Nisbett et al., 2001; Kim et al., in press). By contrast, in collectivistic cultures, such as in many parts of Asia, the dominant model of the self is an interdependent self who is a flexible, connected entity who is bound to others, who conforms to relational norms, and who views group goals as primary and personal beliefs, needs, and goals as secondary (Markus and Kitayama, 1991). In these cultures, relationships also assume an interdependent form — they are viewed as less voluntary than in individualistic cultures and more "given." Within collectivistic cultures, people are more holistic in their cognitive styles than in individualistic cultures and are more likely to attend to the social context (Nisbett et al., 2001; Kim et al., in press).

These cultural differences in social and cognitive orientation have implications for whether people use social support, the mode of social support they use, and the effectiveness of social support seeking. These cultural differences can lead to differences in the use and effectiveness of social support by affecting many of the processes that a person goes through in seeking support: recognizing a stressor, experiencing emotions related to the stressor, deciding whether to express a need for support, and ultimately, requesting help from others (Bolger and Amarel, 2007). Across many different types of stressors, including academic, social, and health stressors, Asians and Asian Americans are less likely to seek social support to cope with stressors than are European Americans (see Kim et al., 2008 for a review). This cultural difference has been observed both in self-reported use of social support as well as in support seeking behavior in dyadic interactions (Sherman et al., 2009). Moreover, for European Americans, social support seeking is associated with greater resolution of the stressor, whereas for Asian Americans, social support seeking is associated with *less* successful resolution of the stressor (Kim et al., 2006). In the present article, we examine several psychological factors that are related to these cultural differences in support seeking, and research that has been conducted on their neural bases and biological impact.

Cultural differences in attention to context

A person who asks a friend for help, for example, by requesting a ride to the airport, may be attending primarily to the problem (a need for a ride) and the solution (the friend who can drive). However, a person who decides not to ask the friend for help, but rather, decides to take the bus to the airport, may be attending more to the situational context facing his or her friend. The bus taker may be aware of constraints on the friend's time, and the potential inconvenience that asking for a ride could cause. Thus, differences in attention to contextual factors could play in a role in deciding to seek social support.

Of course, in the above example, people may have different motivations (i.e., to receive comfort, or to not burden a friend) that may influence how they perceive the availability of the friend and their willingness to ask for help. However, we propose that cognitive distinctions in terms of locus of attention are relevant as well, and suggest one reason why cultures may differ in seeking support. These cognitive differences could manifest themselves in cultural differences in paying attention to the focal event versus paying attention to the social context. Consistent with this possibility research findings on culture and cognition have demonstrated that Asians and Asian Americans pay attention to situational factors more than European Americans do, as they are more attuned to the background of a focal object and the social context of an event (Ji et al., 2001; Masuda and Nisbett, 2001; see Nisbett et al., 2001 for a review). For example, in one study, Japanese participants were more likely than European American participants to attend to and recall contextual factors when viewing underwater or nature scenes, whereas European Americans were more likely to attend to and recall aspects of the focal object (Masuda and Nisbett, 2001). These cultural differences are rooted in differences in basic perceptual processes. In a study that measured the eye movements of American and Chinese participants, the Americans fixated on the focal object, whereas the Chinese made more saccades, that is, rapid eye movements, to the background (Chua et al., 2005).

What are the neural correlates of these cultural differences in attention? Previous research has found that East Asians perform better on tasks with contextual demands, whereas European Americans perform better on context-independent tasks (Kitayama et al., 2003). Building on these findings the researchers (Hedden et al., 2008) conducted a functional imaging study comparing cultural groups during such tasks to provide convergent evidence and examine the neural underpinnings of these attentional differences. Increased activation in frontal and parietal brain regions was associated with attentional control when participants engaged in the culturally incongruent tasks, that is, context-dependent tasks for European Americans and context-independent tasks for Asian Americans (Hedden et al., 2008). Thus, similar brain regions were activated among people from different cultures during the culturally non-preferred activity, which indicates that greater attention may be needed for those activities (Hedden et al., 2008). This study raises intriguing questions about the neural pathways underlying attentional focus during social support interactions. For example, one possibility is that it requires greater attention for European Americans to focus on contextual factors when deciding whether or not to seek support. Not seeking support because a support provider is burdened could require, for those who do not habitually focus on the context, additional cognitive resources, as in the context-dependent tasks used by Hedden et al. (2008). This possibility was examined directly in a study that compared the effectiveness of culturally preferred versus not preferred forms of social support (Taylor et al., 2007), a study we shall describe in a later section.

Within a social support transaction, one relevant contextual factor concerns the potential provider of support. A study by Coan et al. (2006) examined whether different neural regions associated with threat are activated depending on from whom a person is seeking support. In the study, female participants anticipated possible electric shock while in the scanner; in a within-subjects design, the women were either threatened with shock or not and either held their husband's hand, a stranger's hand, or engaged in no hand-holding. Thus, this study provides an opportunity to examine whether people are sensitive to the type and quality of the relationship between the support provider and support recipient.

The shock (vs. no-shock) trials revealed increased activation in a network of brain regions associated with threat, pain, and negative affect, including the ventral anterior cingulate cortex (vACC), right dorsolateral prefrontal cortex left caudate (RDLPFC), superior colliculus, posterior cingulate, left supramarginal gyrus, and right postcentral gyrus. These same regions showed reduced activation during threat when the participants held the hands of their husband or a stranger, relative to no hand-holding (Coan et al., 2006). Although there was strong similarity between the two hand-holding conditions in threat-reducing effects, areas related to emotion regulation centers (such as RDLPFC and caudate) showed attenuated activation in the spouse condition than in the stranger condition. Finally, marital quality moderated the relationship between spousal hand-holding and neural threat response, as those with higher marital quality had less threat-related activation in the right anterior insula, superior frontal gyrus, and hypothalamus, suggesting that people are sensitive to the quality as well as the type of relationship when seeking support (Coan et al., 2006).

Although culture was not examined in the study by Coan et al. (2006), based on the analysis just offered, one might expect that Asian Americans would be more affected by the differences in whether a close other versus a stranger held their hand. Our research has demonstrated that in deciding whether to seek social support, Asians and Asian Americans are more sensitive to relational constraints than are European Americans. Asians and Asian Americans believe that seeking help can negatively affect the harmony of the group, can make other people concerned for them, and raises fears that they could lose face with others by asking for social support (Taylor et al., 2004). An important aspect of the interdependent notion of the self, then, is a greater concern and awareness about one’s impact on close others.

Asian Americans are also more affected by the nature of the relationship that is activated to meet social support needs than are European Americans (Kim et al., 2006). Several studies have shown that Asian Americans are less likely to seek support when a closer relationship is primed than when a more distant relationship is primed, whereas European Americans seek the same amount of support regardless of the prime (Kim et al., 2006). This difference occurs because of Asian Americans’ concern about the negative relational implications of support seeking, that is, their greater attention to the context within which the support-seeking act occurs. European Americans, by contrast, seem to focus less on context, and more on the focal issue, the problem or stressor requiring support or assistance.

If Asian Americans are more attuned to the context facing potential support providers, then they may modulate their support seeking to a greater extent when potential support providers are themselves occupied, relative to European Americans. This hypothesis was examined in a recent study (Sherman et al., 2009) with European American and Asian American romantic couples. One partner prepared and delivered a speech, a stressful task, and their partner, the potential support provider, was given an easy or a difficult task to perform at the same time. The Asian Americans were more impacted than the European Americans by this manipulation: They sought support (i.e., asked for help and/or consolation) when their partner had an easy task, and presumably, more resources to help, but did not seek support when their partner had a more difficult task and was presumably more taxed. The European Americans, by contrast, sought help to the same extent regardless of what their partner was doing. This study provides behavioral evidence that Asian Americans are more attentive to contextual factors than European Americans when considering whether or not to seek social support.

Cultural differences in the importance of expression

The research on attention to context indicates that greater social and contextual awareness can affect whether a person seeks social support. Intrapersonal factors are also relevant in deciding to seek support. When a person experiences stress, how that person feels about expressing thoughts, and how much emotion the person is willing to express to others, could determine the amount and type of social support the person seeks. Considerable research has examined cultural differences in the value an individual places on expression of thoughts and the process of emotion regulation.

Cultural values of expression

Expressing one's thoughts and feelings may feel to some people like an automatic, natural response, but to others, it may feel effortful and distracting. Indeed, the very notion of expression is viewed and practiced differently in different cultures. In more individualistic cultures, the expression of thoughts, preferences, and needs is viewed as an expression of selfhood, and thus, freedom of expression is a sign of individual freedom and an independent self. By contrast, in more collectivistic cultures, private and internal thoughts are relatively insignificant in defining the self, as roles and relationships are readily recognizable by others without being expressed (Kim and Ko, 2007). In this context, self-expression may not convey core aspects of the self, and an act of expression may not have the same implications for the self. The appropriateness and desirability of expressing one's thoughts and feelings when in need, then, may vary considerably as a function of an individual's cultural context.

Research supports this theorizing about cultural differences. European Americans value verbal expression to a greater extent than Asian Americans (Kim and Sherman, 2007; Ashton-James et al., 2009). European Americans also become more invested in their choices when they are allowed to express their preferences compared to Asian Americans (Kim and Sherman, 2007). These cultural differences in the value of expression have cognitive and biological effects as well. In a series of studies, Asian American participants completed a cognitive problem-solving task either in silence or while verbalizing their thoughts, and their performance and cortisol response to the task were measured (Kim, 2002, 2008). The verbalization of thoughts consistently impaired the cognitive performance of Asian Americans, but not the performance of European Americans. The results also indicated that verbalization led to significantly lower cortisol levels [an indicator of stress-related hypothalamic pituitary adrenocortical (HPA) activation] in response to the problem-solving task among European Americans, but did not yield such benefits to Asian Americans (Kim, 2008). Thus, for European Americans, talking can reduce stress, and this may account for their greater expressivity in the form of support seeking when they experience stress.

Emotion regulation

Asking for help, particularly for emotional problems, leads people to reveal their emotions. Cultural differences in emotion regulation strategies, then, could lead to differences in support seeking. For example, Gross and John (2003) have shown that Asian Americans are more likely to report using emotion regulation strategies of suppression than European Americans. People are also less accurate in judging the emotions of Asian Americans than European Americans (Okazaki, 2002), suggesting that Asian Americans may regulate their emotions by not exhibiting distress that could be picked up by others. Indeed, Asian Americans consider the expression of negative emotions with casual acquaintances as less appropriate behavior than do European Americans (Matsumoto, 1993).

Within European American cultural contexts, utilizing suppression as an emotional regulation strategy is associated with both personal and social costs. Emotional suppression leads to decreased memory (Richards and Gross, 1999), and is associated with decreased likability within one's social group, reduced social support, and decreased relationship closeness (Gross and John, 2003; John and Gross, 2004). Within dyadic interactions, suppression by one person led the other person to have increased negative feelings about the interaction and worse coordination among the interaction partners (Butler et al., 2003). However, Asian Americans do not seem to experience the same interpersonal costs of emotional suppression as do European Americans

(Butler et al., 2007). These findings suggest that, in a cultural context that values personal reserve over personal expression, emotional suppression may be less costly.

Recent research examining the neural basis of different emotion regulation strategies may have implications for these cultural differences. Research on two emotion regulation strategies, cognitive reappraisal and suppression, suggests that cognitive appraisal is instigated earlier than emotional suppression (Goldin et al., 2008). Using functional MRI, the researchers found that instructions to reappraise disgusting images led to prefrontal cortex activity earlier and decreased amygdala and insular responses, whereas instructions to suppress the emotion produced prefrontal cortex activity later, but with increased amygdala and insula responses. Other research has found that another emotion regulation strategy, labeling one's affective responses during negative emotional experiences diminishes activation of the amygdala and other limbic regions (Lieberman et al., 2007). Both findings are potentially related to social support seeking to the extent that talking about affective experiences is a way in which people seek support and suppression of emotions is a way in which people cope without seeking social support.

As the neural pathways and temporal sequences underlying different emotion regulation strategies are elucidated, an important question centers on how individual and cultural differences may moderate these processes. Mauss et al. (2008) propose that people vary in their automatic, that is, non-deliberative, responses to emotional-provoking situations, in part, through the activation of different knowledge structures, schemas, and norms. Culture plays a key role in determining and shaping the knowledge structures that are activated in different emotional-evoking situations (Kitayama et al., 2004), and thus different emotional regulation strategies may be automatically activated as a function of an individual's cultural context.

This approach suggests some future directions for research examining the neural basis of emotion regulation strategies. For example, if suppression is a more habitual response for Asian Americans (Butler et al., 2007), then there may be a different time course for the activated brain regions for this emotion regulation strategy among Asian Americans than for European Americans and they may not experience an increase in amygdala activity when they use this strategy (Goldin et al., 2008). Questions of this sort represent an exciting line for researchers interested in integrating cultural and neural approaches.

Culture and different forms of social support

Social support has clear beneficial effects. It can reduce the likelihood of illness, speed recovery from illness when it does occur, and reduce the risk of mortality from serious disease (Berkman and Syme, 1979; House et al., 1988). Higher levels of social support have been tied to reduced cardiovascular reactivity and HPA axis activity to laboratory stressors (e.g., Eisenberger et al., 2007; Uchino et al., 2001). Indeed, social support is one of the most effective ways by which people protect themselves from the adverse mental and physical health effects of stress (Taylor, 2007).

Still, research has documented some costs to drawing on the social network for help, and considerable research indicates that the mere perception that social support is available is sufficient to engage many of its benefits (see Taylor, 2007, for a review). When people are experiencing stressors, sometimes the support network can only be imagined (Smith et al., 2004). People think of their families during difficult times at work, or look at pictures of their children when they are away from home. This aspect of social support, it is important to point out, does not require the verbal expression or disclosure that characterizes the more explicit support seeking of asking for instrumental help or emotional consolation that yield the cultural differences previously described (Kim et al., 2008).

Accordingly, we contrast *explicit social support*, people's specific recruitment and use of their social networks in response to specific stressful events, with more *implicit social support*, which we define as being in the company of close others without disclosing or discussing one's problems vis à vis specific stressful events. Implicit support can also take the form of reminding oneself of close others; this conceptualization particularly emphasizes the absence of explicit disclosure and sharing of the stressful events.

Neural pathways for social support effects

An important question, then, is how social support can buffer people when supportive networks are absent. People may reflect upon their social support networks, and research has shown that thinking about supportive ties (relative to acquaintances) can be sufficient to reduce heart rate and blood pressure responses during acute laboratory stressors (Smith et al., 2004). Eisenberger et al. (2007) also examined whether people who interact with more supportive others on a daily basis experience reduced stress responses during threatening tasks. Using an experience sampling paradigm, participants were beeped at random intervals over a 9-day period and reported how supportive their most recent interaction partner was; support was summed, yielding a measure of supportiveness of their social networks. Participants then came to the laboratory and engaged in a virtual ball tossing task while in the scanner that led them to feel socially excluded; this task has been associated in previous research with distress and increased activation in threat regions of the brain including the dorsal portion of the anterior cingulate cortex (dACC; Eisenberger et al., 2003). In the third part of the study, participants engaged in the Trier Social Stress Test (Kirschbaum et al., 1993) and had to give a speech and engage in a mental arithmetic challenge in front of a hostile audience. Salivary cortisol levels were assessed before and after these challenging tasks. People who reported more supportive social networks had lower cortisol levels during the social stress task than people with less supportive networks, even though their networks were not physically present in the laboratory during the stressful activity.

The researchers then examined the relationship between the supportiveness of the social network, neural activation during social exclusion, and cortisol reactivity during the social stressor. People with more supportive social networks had reduced dACC activation during the social rejection task as well as reduced cortisol levels during the social stress task. Furthermore, the individual differences in dACC activation mediated the relationship between having a supportive social network and stress-reactivity during the lab stressor, providing evidence as to one neural pathway by which social support can reduce stress (Eisenberger et al., 2007).

Based on the cultural analysis offered earlier, one would predict that Asians and Asian Americans would be especially benefitted by social support that involves awareness of and reflection on supportive ties (i.e., by implicit support) but not by explicit social support that involves asking for aid or solace. By contrast, European Americans may benefit more from the explicit seeking of solace. To test these predictions, Asian Americans and European Americans (Taylor et al., 2007) were primed with different forms of support prior to engaging in a lab stressor (Kirschbaum et al., 1993). They were instructed to think about a group that they are close to and write about the aspects of that group that are important to them (in the implicit support condition) or to think about people they are close to and to write a letter directly asking for advice and support for the upcoming tasks from one of these people (in the explicit support condition). Participants in no support control condition completed a neutral writing activity. After the writing task, participants engaged in the stressful lab tasks; cortisol levels were assessed from saliva samples before and after the task.

Asian Americans who merely wrote about a group that they are close to without asking for help reported less stress and had lower cortisol levels following the stressors than Asian Americans who explicitly wrote to close others and sought support. Explicit support led European Americans to experience less stress and have lower post-task cortisol levels than did implicit support. In fact, the results suggest that the culturally inappropriate form of social support (i.e., explicit for Asian Americans and implicit for European Americans) actually exacerbated stress.

The distinction between implicit and explicit support, and its differential effects on stress-reactivity as a function of culture, suggest important questions for future research examining the neural pathways of social support. For example, consider the measure of social support utilized in the Eisenberger et al. (2007) study that found associations between social support and reduced dACC activation during a social rejection task. The study asked participants about the supportiveness of their recent contacts. The culture and social support research suggests that different types of support may be seen as most supportive and may have influenced those judgments. European Americans may have felt most supported after receiving explicit support, whereas Asian Americans may have felt most supported after merely being in the company of close others without disclosing a stressor. Thus, there may be similar associations between possessing a socially supportive network and reduced biological responses to stress, but what is considered a socially supportive network may be moderated by culture.

Genes X culture interactions in social support use

To date, research on the interaction of cultural and biological bases of social support has focused on how culture moderates biological responses, such as how different types of social support affect people during stress as a function of their culture (Taylor et al., 2007). An alternative approach is to examine how biological factors, such as genetic predispositions, can interact with culture in leading people to pursue social support. We have begun to examine these questions by focusing on the serotonin system, in which certain polymorphisms have been associated with different emotional regulation patterns, especially in stressful life situations (Caspi et al., 2003; Lenze et al., 2008; Taylor et al., 2006).

Studies focused on the serotonin transporter polymorphism (5-HTTLPR) have found a greater propensity for distress in high stress circumstances among people with a particular variant, the s/s genotype (e.g., Caspi et al., 2003); this s/s genotype occurs in disproportionately high frequency among Asians/Asian Americans relative to European Americans (Gelernter et al., 1997). One study examined the propensity to experience depressive affect as a function of the supportiveness of their environment among participants including Asian Americans and European Americans (Taylor et al., 2006). People who were s/s genotype (and who were disproportionately Asian Americans) were more likely to experience depressive affect when they grew up in a stressful environment, but in a significant reversal, experienced a greatly reduced risk of depressive affect if they grew up in a supportive environment. These findings suggest that the supportiveness of the family environment could significantly offset a genetic risk for distress that may be especially experienced by Asian Americans. Given these findings, it may be the case that the well-documented tendency of interdependence among Asians (Markus and Kitayama, 1991) may have arisen in part to modulate potential genetic risks, for example, the higher frequency of s/s genotype in Asian populations (Taylor et al., 2007).

In addition to this idea of gene-culture coevolution, another possibility to consider is the interaction between the gene and culture, that is, how culture moderates the behavioral outcomes of genetic predispositions. In one recent study (Kim et al., 2009), we examined the cultural and genetic basis of the use of social support, focusing on a serotonin 1A receptor gene (5-HTR1A) and the oxytocin receptor gene (OXTR). 5-HTR1A is an autoinhibitor of serotonin release, and the G allele of the polymorphism prevents binding of putative repressor proteins (Huang et al., 2004; Lemonde et al., 2003). The G allele is associated with greater proneness for an array of psychological disorders, such as depression and anxiety disorder (Huang et al., 2004; Lenze et al., 2008). A few studies have examined the connection between OXTR gene and social behavior phenotypes; one animal study shows that mice with a null mutation in the OXTR gene tends to be more aggressive (among males), less maternally nurturing (among females), less distressed by social isolation, and have impaired social memory (Takayanagi et al., 2005). The amount of research on this polymorphism with humans is relatively limited, but one study shows that the frequency of the A/A genotype for SNP rs53576 was higher among autistic individuals (Wu et al., 2005).

Similar to the case of 5-HTTLPR, we found the gene by environment interaction with 5-HTR1A (Kim et al., 2009). Individuals with the G/G genotype showed a greater association between the degree of environmental risk and psychological distress, compared to individuals with the C/G genotype, who in turn showed a greater association than individuals with the C/C genotype. Given this finding, we examined the roles of culture and OXTR in influencing the use of social support. We found that European Americans with the G/G genotype of OXTR reported seeking greater social support as a function of distress experienced, compared to the G/A or A/A genotypes. By contrast, Koreans with the G/G genotype did not seek social support as a function of stress any more than those with the other genotypes, as it is not the culturally normative way in which people cope with their stress and affiliate with close others. In summary, we obtained a gene X culture interaction in social support use. It appears that those who are more genetically affiliation-prone seek social support more, but only when it is a culturally sanctioned way of coping (Kim et al., 2009). These findings demonstrate the importance of examining the interaction of genetic and cultural influences in conjunction with documented cross-cultural differences.

Conclusions

The impact of social support on health and well-being has stimulated considerable research on its neural underpinnings and biological impact. Research has also uncovered profound cultural differences in how social support is experienced. Culture plays a large role in the decision to seek social support, the form in which social support is sought, and the extent to which social support can attenuate stress. Moreover, recent research has begun to examine the neural underpinnings of processes highly relevant to social support, such as how people see the self in relationship to others, the distinction between possessing an analytic or holistic cognitive style, the value of expression, and how people regulate their emotions.

In the present review, we aimed to connect research on social support and related processes from multiple perspectives. In so doing our goal was to not only integrate different levels of analysis, but to show how they interact with each other in determining the use and effectiveness of social support. The integration of health psychology, cultural psychology, social neuroscience, and genetics in the study of social support is in its early stages. Although elements of these approaches have been integrated in some studies, an overarching framework that incorporates these multiple perspectives has yet to emerge. The present review represents an attempt to develop such a framework.

Acknowledgments

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SECTION VI

Applications of Cultural Neuroscience

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CHAPTER 17

Neuroeconomics: in search of the neural representation of brands

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Abstract: In modern economy the customer is confronted with a huge amount of consumer goods. In this situation, culturally based brands seem to play an important role in establishing strong emotional bonds between customers and goods and to guide people's economic behavior by biasing selections and preference decisions based on affect. Recently, neuroscientific approaches have demonstrated that cultural objects like brands or brand-related behavior may successfully be investigated with neuroimaging tools like fMRI. First studies suggested that structures associated with the reward circuit (striatum) and the dorsolateral part of the prefrontal cortex may be involved when perceiving a favorite brand. Hence, brands that have been associated with appetitive stimuli due to marketing efforts or cultural factors seem to engage similar brain networks than artificially associated reward stimuli. However, brands have different and complex meanings in our life far beyond representing objects of desire. For example, the possession of goods from certain kinds of brands often is used to mark the social state of the owner and to distinguish him or her from other groups. In particular, luxury goods often seem to have this function. Recent neuroimaging results support this observation by showing that viewing logos of luxury brands is associated with brain activity in the anterior medial prefrontal cortex, a region known to be associated with self-centered cognitions. Thus, it seems that brands of luxury goods improve self-relevant thoughts, pointing to the role of luxury brands to mark the superior position of the owner in society. These results demonstrate that cultural symbols like brands can successfully be examined with neuroimaging approaches. Thus, along with advanced cultural theories, neuroeconomics may provide important contributions to the understanding of brand-related or economic behavior.

Keywords: cultural objects; prefrontal cortex; brands; fMRI

Introduction: brands as cultural symbols

In 1998, the car manufacturers BMW as well as Volkswagen aimed to buy the "Rolls-Royce/ Bentley" company. The struggle went on for several months. Finally, Volkswagen managed to buy the brand "Bentley" and the factory of "Rolls-Royce/Bentley" in England. In contrast, BMW only received the rights to use the brand "Rolls-Royce" for about 50 mio euros — without any factories or other material counterpart. However, despite this huge price, experts treated the BWM group as the winner of this deal because they could use the famous brand "Rolls-Royce," whereas Volkswagen received the less value

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brand "Bentley" and some older factories. So why do companies pay so much money just for the right to use a name and a logo, even if everybody knows that the owner of the brand has changed? What is going on in our brains when we see a popular brand?

Brands can be defined as culture-based symbols, which promise certain advantages of a consumer good to the customer. This implies that brands may have different meanings or brand images for different cultures. A different culture does not necessarily mean a different country. Hence, brands even may have different meanings for certain groups in society. For example, clothes of a brand that symbolizes value products for adult people often have completely different connotations for young people. Furthermore, sometimes the image of a brand is not fixed but changes over time. Thus, the meaning of a brand may change very dynamically over time and subjects. The main reason for this seems to be that brands are prone to cultural factors like fashion or marketing campaigns. Therefore, we describe brands here as complex cultural symbols. However, it still remains an issue how brands affect people's choices.

Investigating brand-related behavior with neuroimaging tools

Brands seem to play an important role in establishing strong emotional bonds between customers and consumer goods and guide people's economic behavior by biasing selections and preference decisions based on affect. Marketing experts use highly sophisticated tools to assess subjects' attitudes toward certain brands and obtain information about the image of a brand. In spite of those efforts, these analyses often fail to predict the success of brand products.

Only recently, neuroscientific approaches have demonstrated that cultural objects like brands or brand-related behavior may be also successfully investigated with neuroimaging tools. In particular, functional magnetic resonance imaging (fMRI) seems to be a powerful tool to understand what happens in the brain when we see a famous brand. Furthermore, other techniques like positron emission tomography (PET, Smith et al., 2002), electroencephalography (EEG, Astolfi et al., 2008), or magnetoencephalography (MEG, Ambler et al., 2004; Braeutigam et al., 2004) have also been used to examine economic behavior or neural representations of brands.

Most studies using imaging tools examined economic behavior of subjects under different circumstances. For example, many approaches focused on neural correlates for economic decision processes in social interaction experiments, such as the prisoners' dilemma or the ultimatum game (e.g., Rilling et al., 2002; Sanfey et al., 2003). Other studies investigated trust in economic interpersonal relationships (McCabe et al., 2001; Fehr and Gächter, 2002; Delgado et al., 2005; King-Casas et al., 2005; Kosfeld et al., 2005; Moll et al., 2006).

In one of the first fMRI-studies on cultural objects, Erk et al. (2002) revealed that cultural objects associated with wealth and social dominance modulate the neural reward circuitry. In this study, they examined brain responses to different types of cars and demonstrated that structures of the reward circuit are involved when viewing pictures of sports cars in contrast to pictures of small cars or limousines. The authors considered cultural objects like sports cars as social reinforcers, signaling wealth and social dominance. However, the study focused on global pictures of different car types. Thus, they eliminated all brand information of the objects. Hence, rather than specific brands, the design or the shape of generic sports cars seemed to activate the reward circuit.

So far, only few studies explicitly examined brain responses to the perception of different kinds of brands (e.g., McClure et al., 2004; Schaefer et al., 2006; Schaefer and Rotte, 2007a, b; Koeneke et al., 2008). This review will focus on studies examining the representation of brands or brand-related behavior in the brain.

Brands as somatic markers

It seems reasonable to assume that the prefrontal cortex plays a crucial role when preference decisions are biased by brand information. In his somatic marker hypothesis, Damasio suggested that external or internal stimuli initiate a state that is associated with pleasurable or aversive somatic markers (Bechara et al., 1994; Damasio, 1994, 1996). Somatic markers might be crucial for decision-making even when there is no advantage or disadvantage associated with the response alternatives. Thus, these markers may function to guide the person's behavior by biasing selections. The role of the ventromedial prefrontal cortex (VMPFC) seems to be crucial for this theory because this area stores information about past rewards and punishments (Damasio, 1996). By demonstrating dense interactions with limbic structures in a variety of behavioral contexts this theory has gained much support (Price et al., 1996; Greene et al., 2001; Wagar and Thagard, 2004). In particular, many studies were able to link the VMPFC to reward expectations (e.g., Watanabe, 1996; Knutson et al., 2003; O'Doherty et al., 2003; Paulus and Frank, 2003; Knutson and Cooper, 2005; Kable and Glimcher, 2007).

We hypothesized that brands may function as those kinds of external stimuli that initiate a state with pleasurable or aversive somatic markers (Schaefer et al., 2006). Thus, brands might act as somatic markers, working as unconscious hunches that spontaneously and fast influence subjects' attitudes even before subjects are asked to perform a preference judgment task. We further hypothesized that areas in the prefrontal cortex are involved in generating somatic markers and are activated by familiar brands. To test this hypothesis, we conducted an fMRI study (Schaefer et al., 2006). During fMRI scanning, we showed the participants different logos of brands of car manufacturers that were either well known or unfamiliar to the culture of the subject. Since somatic markers should be active before considering possible advantages or disadvantages of a decision, we did not create a forced-choice paradigm in which subjects have to decide for one product in favor of another. Instead we instructed subjects to imagine driving a car of the presented brand. If they did not know a brand, they were told to imagine driving a generic car. Since somatic markers are working as unconscious hunches, we expected the activation of these markers spontaneously and fast. Based on the theory of Damasio, we hypothesized an activation of the VMPFC when seeing a strong familiar brand. This would support the view that the way brands affect our behavior might be described with the idea of somatic markers.

However, the results showed activation of a region in the anterior medial prefrontal cortex (AMPFC), but failed to show any activation in the VMPFC (Fig. 1). We discussed the results as self-relevant processing induced by the imagined use of cars of familiar brands (see below). Furthermore, other and subsequent studies also did not report activation in the VMPFC when subjects perceived brands (McClure et al., 2004; Schaefer and Rotte, 2007a, b).

For example, in one of the first important studies that explicitly focused on the impact of specific brands on cortical processing, McClure et al. (2004) also used an fMRI approach. The authors reported neural correlates for culturally familiar drinks and suggested two separate brain systems involved in generating preferences. On one hand, activity in the VMPFC predicted people's preferences when judgment decisions were solely based on sensory information, for example, the taste of a favorite drink. On the other hand, a circuitry including dorsolateral prefrontal cortex (DLPFC), hippocampi, and midbrain was engaged when subjects' preference judgments were based on brand information. Thus, preference judgments may be biased by two separate neural networks, based on either sensory or cultural information. The authors suggested that the DLPFC may interact with the ventromedial region of the prefrontal cortex, but it remained unclear how both networks might interact in detail.

Nevertheless, further studies are required to understand the function of the VMPFC for brand-related behavior and the appropriateness of the somatic marker theory for the understanding of how brands affect our behavior.

Neural representation of favorite brands

Since brands can be described as cultural symbols, the effect of a single brand on subjects differs with

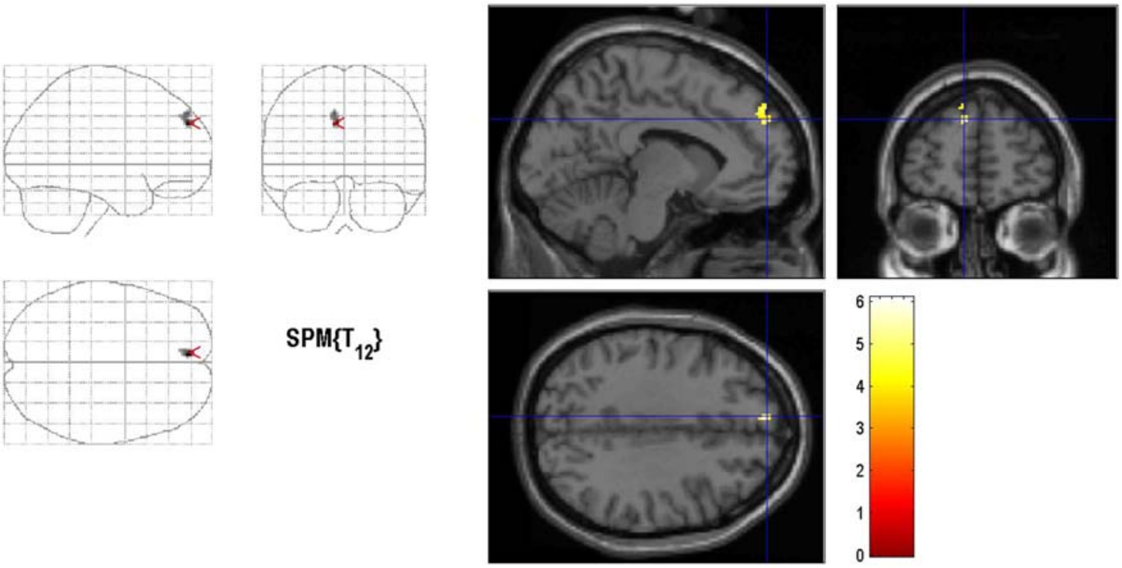

Fig. 1. Brain responses of familiar brands compared to unfamiliar brands. Results revealed activation of the AMPFC for familiar brands. Areas of significant BOLD-signal change are shown as color overlays on the T1-MNI reference brain. The colored bar indicates the T-statistic of the activation. Please see online version of this article for full color figure.

Fig. 2. Examples of familiar brand logos of European car manufacturers presented in the experiment.

their preferences. Hence, one person may favor a specific brand while someone else dislikes it. Thus, in another fMRI study, we aimed to examine the neural representations of favorite brands (Schaefer and Rotte, 2007a). We employed fMRI to measure subjects' brain activity while presenting them logos of different car brands. We hypothesized that brands (and not only generic pictures of status symbols, like sports cars) may function as reward stimuli and therefore modulate the reward circuit. Hence, we assumed that brands with positive connotations to the subjects may be associated with activation of structures related to the reward circuit. Since different subjects prefer different cultural objects, we hypothesized that only brand subjects *individually* rated as their favorites act as reward stimuli. Subjects were lying in the fMRI scanner and viewed 14 pictures of trademark-logos of well-known European car manufacturers (Fig. 2). All logos contained the name of the brand and were compatible regarding the size of the image. After the experiment, we asked the participants to rate the seen brands according to their personal attractiveness.

The fMRI results demonstrated activation of the ventral striatum (putamen) when subjects saw a personal attractive brand compared with a personal unattractive brand (Fig. 3). Thus, the

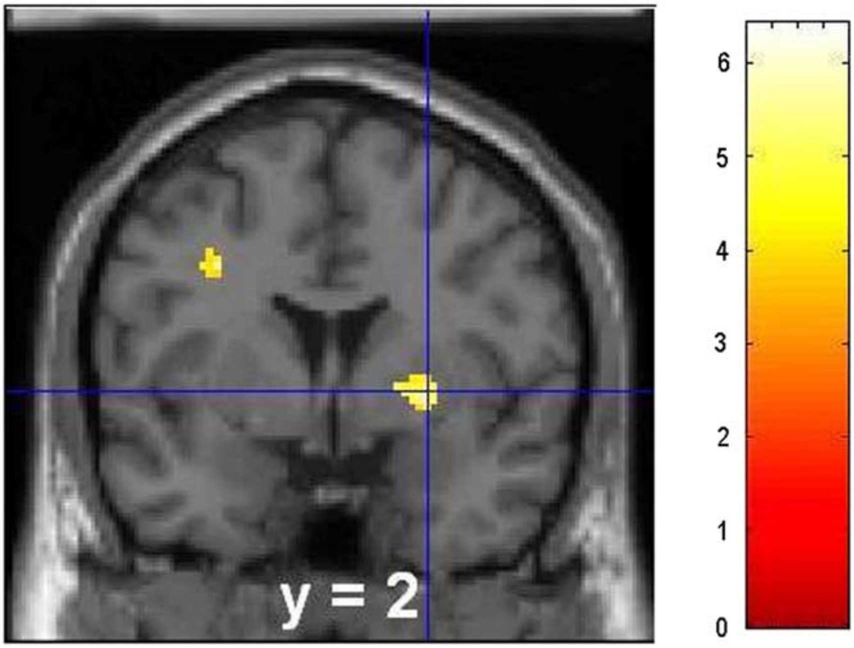

Fig. 3. Neural correlates of favorite brands compared to nonfavorite brands. Results showed activation of the DLPFC and the ventral striatum (putamen). A coronal slice through the ventral striatum is shown.

results demonstrate that the mere imagination of using a product of a favorite brand engages similar reward-related areas than stimuli artificially associated with appetitive rewards due to classical or instrumental conditioning in an experimental context (e.g., O'Doherty et al., 2004a, 2006). This supports the notion that brands may have been associated with rewarding or appetitive stimuli through the process of classical conditioning due to advertising efforts (Gorn, 1982). As a consequence, even the mere perception of a personally preferred brand logo is sufficient to activate structures of the reward circuit.

However, some of the presented car manufacturers never do any advertising at all (e.g., Ferrari, Rolls-Royce). This points to the fact that advertising is only one dimension in the development of people's choices and preference set. Furthermore, as the following paragraphs try to underline, goods can be preferred not only because one likes them personally.

Results of the just-mentioned study also revealed activity in the DLPFC when subjects viewed favorite brands. Activation of this brain structure is known to reflect aspects of cognitive control and working memory. Several studies suggest that the DLPFC may be important for employing affective information in biasing behavior (Davidson and Irwin, 1999; McClure et al., 2004). Thus, a network of areas in the prefrontal cortex and the striatum seems to be important for the representation of favorite brands.

Secondary inducers of reward: social incentives

When choosing appropriate actions to receive rewards, the brain needs to form associations between external stimuli, action selections, and rewards. Numerous studies have shown that the striatum plays an important role for this kind of learning (Pagnoni et al., 2002; Haruno and Kawato, 2005). The results reported above are in line with recent studies and point to a role of the ventral striatum in maintaining a representation of the subjective value of the associated reward stimulus (e.g., O'Doherty, 2004b, 2006; Samejima et al., 2005). The reported findings even extend these studies by demonstrating that the mere perception of logos of favorite brands as cultural symbols may modulate regions in the striatum as a function of their characteristics as personal reinforcers.

However, brands are complex cultural objects and people use brands for different purposes. A post hoc covariate analysis between the magnitude of the BOLD signal and behavioral results revealed that activity in the ventral striatum was positively correlated with the attributed sports and luxury characteristics of the chosen favorite brands, but showed a negative linear relationship with the attributed rationality (see Fig. 4). Thus, the reward-related areas showed higher activation when personal favorite brands were rated by all participants as sporty or luxury and lower when they assessed them more as cars of rational choice (or a value car). Hence, not only primary inducers (the personal attractiveness) but also secondary inducers of reward mechanisms based on *social* cognitions and associations seem to modulate reward-related brain areas. Thus, we speculate that there might be primary and secondary inducers of reward. The former may signal fast anticipation of "primary" needs, while the latter may point to satisfaction of more complex desires. When we decide to buy a product, we not only think about personal need satisfaction but also consider what others may think about our decision to buy a car of this brand. Sometimes these thoughts may advise us against our wish and sometimes they may encourage us to do so. For example, a sports car may lead to feelings of enviousness for others. In contrast, a very old and cheap car may put us in a bad light for others. Another example is buying a hybrid car, which may enhance the prestige of the buyer. Thus, there are not only hedonistic primary reasons that influence our decision for a product but also social reasons (at least for non-fast-moving consumer goods). One cortical region where both primary and secondary inducers of reward may interact might be the striatum. However, further research is necessary to validate this speculation.

Brain responses to luxury brands

Previous research has demonstrated that when we see a preferred brand, we seem to anticipate the reward of owing this object of desire

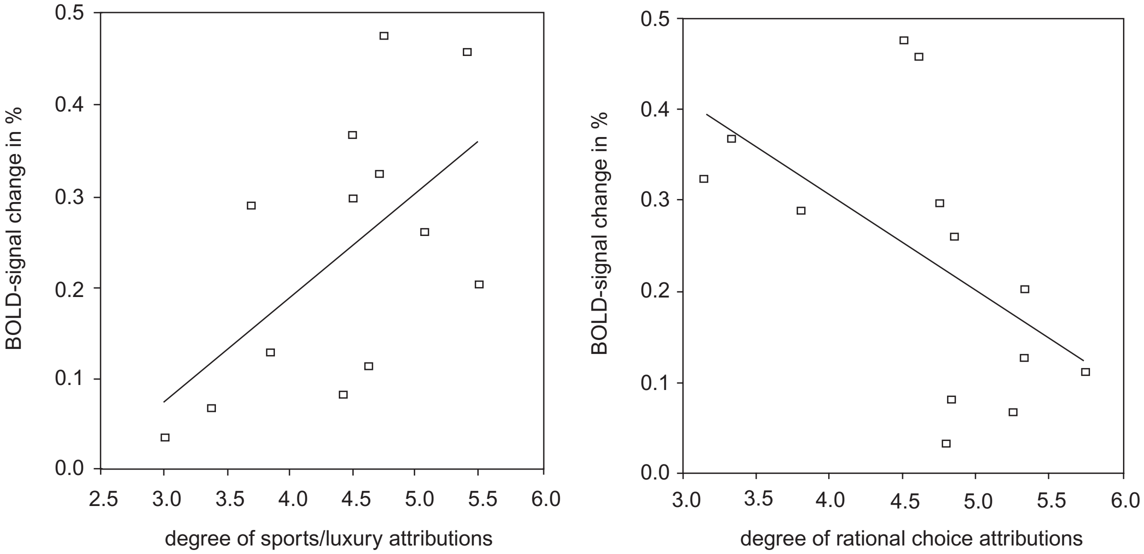

Fig. 4. Scatter plots showing activity in the ventral striatum (putamen) as a linear function of attributed sports and luxury characteristics ($r = 0.59$, $p < 0.03$) and as a negative linear function of attributed rational choice characteristic ($r = -0.67$, $p = 0.01$, Spearman's rho).

(Erk et al., 2002; Schaefer and Rotte, 2007a; Koeneke et al., 2008). However, brands have different and complex meanings far beyond representing objects of desire. Another important function of brands seems to mark the social rank of the owner. In particular, luxury goods often seem to have this function. Whereas in the medieval times the powerful class used valuable clothes and jewelry to show its position in society (Veblen, 1899), at the end of the 18th century the aristocratic system vanished and the attitude toward luxury goods changed. More and more people were working as employees in offices, wearing very similar clothes. Although luxury goods still had the function to mark the position in society, the way to deal with these goods changed. Nowadays, luxury often is more subtle and interacts with behavior and attitudes in defining the position of somebody in society (the *habitus*, Bourdieu, 1979). Moreover, luxury often seems to be coded by certain brands. In contrast to older times when people were fixed to their position in society, today many people can buy products of luxury brands, allowing the owner to pretend a certain social rank. Marketing experts are familiar with this phenomenon and assure that luxury brands retain their image as being a brand for rich and wealthy people, although they also (or in particular) expect few wealthy people to buy those products.

Given this background, we assumed that the neural representation of luxury brands is different from that of brands representing more value products. To test this hypothesis, we examined brain responses to both kinds of brands in an fMRI paradigm (Schaefer and Rotte, 2007b). During fMRI, scanning participants viewed different logos of familiar car brands that were representative for either luxury goods or value products. Based on previous studies, we expected a different engagement of the prefrontal cortex for the perception of luxury brands compared with brands representative for value products. Several recent studies suggested similar functional dissociations in the frontal lobe for the perception of different kinds of brands. For example, McClure et al. (2004) proposed two separate prefrontal sites in biasing preference judgments as a function of either sensory or cultural information. Whereas the former seems to be based on activations in the VMPFC, the latter is supposed to be affected by the DLPFC. Goel and Dolan (2003) demonstrated reciprocal neural responses in the prefrontal cortex during emotionally neutral (“cold”) and emotionally salient (“hot”) reasoning. “Cold” reasoning enhanced activity in lateral and dorsolateral prefrontal cortex and suppressed activation in the VMPFC, whereas “hot” reasoning resulted in suppression of activation in lateral and dorsolateral prefrontal cortex and enhanced activation of the VMPFC (as similar in Gilbert and Fiez, 2004; Krain et al., 2006). Based on these studies, we hypothesized that different categories of brands may activate different cortical networks in the prefrontal cortex (Schaefer and Rotte, 2007b). In particular, the perception of brands that are related to high “social dominance” (luxury brands) should be accompanied by an active network including the VMPFC and other reward-related areas (affective “hot” processes). Value or pragmatic brands, which do not signal social dominance, should activate cortical structures known to be important for cognitive control (in particular the DLPFC), but no regions known to be involved in reward expectations.

Results revealed an active network of bilateral superior frontal gyri, hippocampus, and posterior cingulate, which was related to familiar brands in general. Brain responses to luxury brands showed activations in the AMPFC and the precuneus. In contrast, brands rated as value products activated the left superior frontal gyrus and the anterior cingulate cortex (see Figs. 5 and 6).

Thus, luxury brands (known as social reinforcers and supposedly representing cultural symbols linked to emotional salience or “hot” reasoning) failed to show activity in the VMPFC, a region associated with the processing of affective “hot” stimuli. In contrast, luxury brands elicited activation in the AMPFC and the precuneus. The AMPFC is known to be related to self-centered cognitions, self-reflection, and self-relevant processing (Ochsner et al., 2004; Schmitz et al., 2004; Seger et al., 2004; Moran et al., 2006). For example, Johnson et al. (2002) asked subjects to

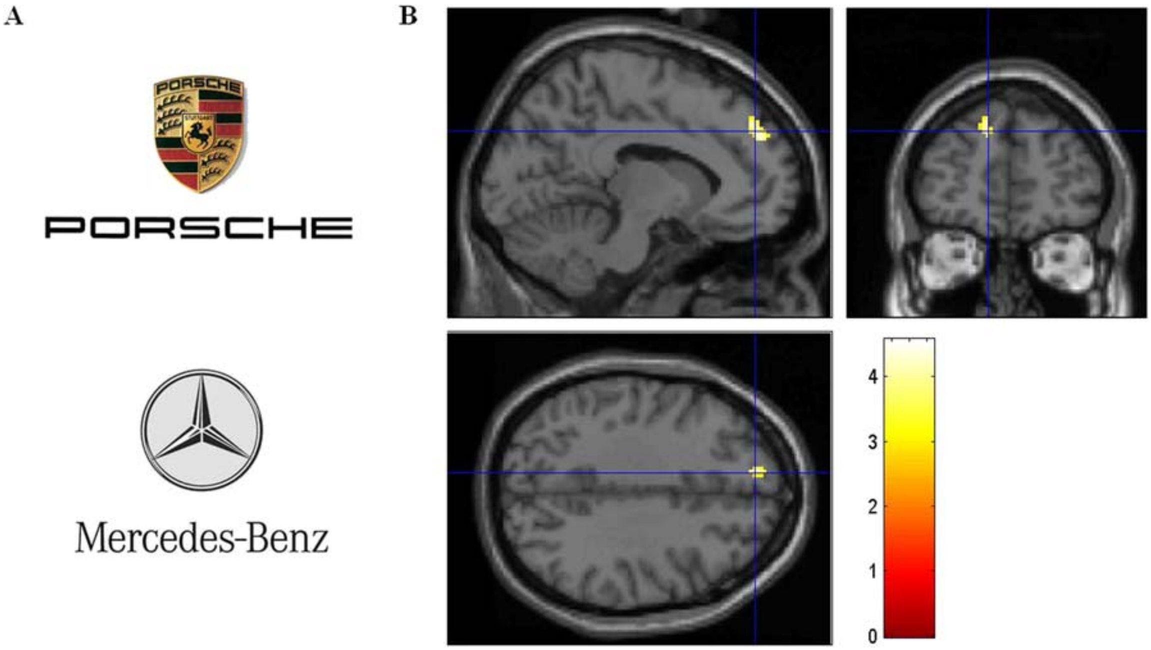

Fig. 5. Brain responses to luxury brands. (A) Two examples of luxury brand logos. (B) Activation of the AMPFC elicited by the presentation of luxury brands as compared to unfamiliar brands.

respond to different statements requiring knowledge of and reflection on their own abilities, traits, and attitudes while scanning their brain activity. Compared to statements about basic semantic knowledge, self-related statements revealed activations in the AMPFC and posterior cingulate. Furthermore, it has been suggested that the precuneus plays a central role for episodic memory retrieval and self-processing operations (Cavanna and Trimble, 2006). Hence, we speculated that luxury brands, which are related to high social values, may have evoked increased self-relevant thoughts in our subjects. Since the randomly chosen set of stimuli in our first study (Schaefer et al., 2006, see above) consisted mainly of luxury brands, the activation of the AMPFC in this earlier study can be related to the luxury characteristic of the presented familiar brands.

Why is the perception of luxury brands associated with cortical activations related to self-centered cognitions? Subjects in our study imagined using a product of the shown luxury brands. We speculate that they might have imagined possessing one of these luxury goods and pictured mentally the situations in which others would see them with these products. Thus, the participants may have imagined being in a more superior position in society than they actually are. These results would confirm earlier theories on the fetish character of goods (Marx, 1867; Lukács, 1972). For instance, Marx (1867) assumed that people in capitalism have an attitude toward goods that is comparable to a fetish in archaic societies. In his theory, he used the term commodity fetishism to describe the belief in capitalist-market-based societies that value inheres in commodities (instead of being added to them through labor).

Ethical aspects

Recent advances in neuroeconomics have been accompanied by a great interest of mass media (Murphy et al., 2008). Although only few peer-reviewed studies on neuroeconomics have been published so far, newspapers and mass media are constantly reporting about any progress in this

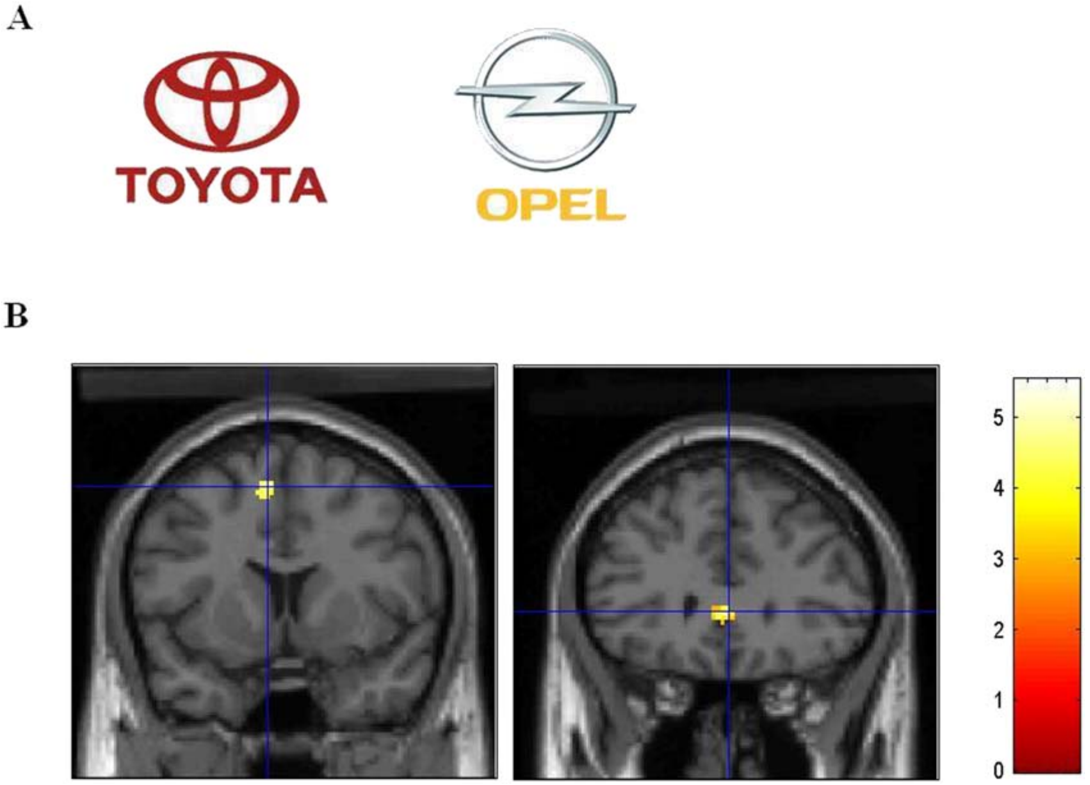

Fig. 6. Brain responses to the perception of value brands. (A) Typical examples of value brands. (B) Activations of the DLPFC and the anterior cingulate cortex elicited by the presentation of value brands as compared to unfamiliar brands logos.

area of research. Why is this issue so much more interesting for many people than other topics in cognitive neuroscience? And why is this research so intensively discussed?

The major reason for the high resonance of this research arises from the possible relevance for economic purposes. Many people criticize neuroeconomics by arguing that techniques that are invented for medical purposes (in particular fMRI) are now misused to learn about more effective marketing efforts and develop strategies making companies more profitable. In particular, people are afraid that by using the new ‘‘brain scanner’’, companies may ‘‘manipulate’’ the consumer.

However, the brain is an extremely complex system. So far, knowledge about the neural representation of brands and about brand-related behavior is very limited. Hence, ideas about ‘‘manipulation’’ are far away from real possibilities of neuroeconomics. Further, fMRI or other neuroimaging approaches cannot simply tell what a company has to do to make the potential customer buy their products. Together with established methods of marketing research, neuroeconomics might be able to help companies to identify products the customer might like. Thus, new brain imaging approaches might supplement established methods, but they will not replace them. Hence, neuroeconomics is just one approach among others. However, a new dimension is reached when we can see that neural activations differ just because of the perception of different brands. Nevertheless, what we see as activations in the brain are the *results* of marketing efforts for years; the new brain imaging methods did not ‘‘manipulate’’ anything.

We believe that economic or brand-related behavior is an important topic for current research in cognitive neuroscience. Understanding how people behave in economic situations is extremely important for both concrete purposes (e.g., understanding economic crisis) as well as basic research. However, it is also essential to keep ethical objections in mind and discuss these issues in a thorough way.

Conclusion and future directions

This chapter outlined first preliminary results showing how brands as complex cultural symbols seem to be represented in the brain and affect brand-related behavior. First studies have shown that the perception of personally favorite brands is accompanied by activations of the reward circuit. Thus, when we view a brand, we seem to anticipate the rewards promised by the brand. Further, recent research has demonstrated that brands are differentially processed in the prefrontal cortex depending on the attributed characteristics of the brand. For instance, luxury brands seem to elicit activation in the AMPFC, a region known to be involved in self-centered cognitions.

These results demonstrate that even complex cultural symbols can be successfully investigated with neuroimaging approaches. Furthermore, studies have shown that neuroeconomics is much more than just telling us that emotion is important in economic decisions. Thus, combined with advanced cultural theories, neuroeconomics may be eligible to show us new ways of thinking about brands and their impact on our behavior. Future directions may focus more on brand-related behavior. In particular, further studies might investigate how different brand representations in the brain interact in economic situations, for example, when finally buying a good or after buying a product (Festinger, 1957). Further, since cultural symbols can also be described as cognitive schemes, using theories focusing on those research topics may be very promising to understand brand-related behavior (e.g., Heider, 1958).

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CHAPTER 18

"Neuroarchaeology": exploring the links between neural and cultural plasticity

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Abstract: This paper aims primarily at two things: The first is to present an overview of the newly developed field of "neuroarchaeology" and discuss its theoretical grounding in Material Engagement Theory (MET) and the extended mind hypothesis. The second is to use the above overview as a basis for advancing some tentative proposals about the role that neuroarchaeology, by placing the mutual constitution of brain, mind, and culture in evolutionary perspective, can play within the field of cultural neuroscience and about the common benefits that can arise out of such a cross-disciplinary coalition.

Keywords: neuroarchaeology; material culture; cognitive archaeology; material engagement; plasticity; distributed cognition

Introduction: what is neuroarchaeology?

Since the emergence of cognitive archaeology in the early 1980s there has been some radical advancements as well as changes in perspective in the way we approach, interpret, and understand the prehistory of mind (e.g., Renfrew and Zubrow, 1994; Renfrew and Scarre, 1998; Renfrew et al., 2009; Renfrew, 2001a, b, 2004, 2007; Knappett, 2005; Stout et al., 2008; Stout and Chaminade, 2007, 2009; Bruner, 2003, 2004, 2007; Mellars and Gibson, 1996; Davidson and Noble, 1989; d' Errico, 1998; Gosden, 2008; Gibson, 1993; Wynn and Coolidge, 2003, 2004; Coolidge and Wynn, 2004, 2005, 2009; Wynn, 2002; Deacon, 1997; Lewis-Williams, 2002; Humphrey, 1998; Hodgson and Helvenston, 2006; Mithen, 1996; Mithen and Parsons, 2008; Noble and Davidson, 1996; Malafouris, 2004, 2007a, b, 2008a–c). Archaeologists have learned a great deal about the social and cultural basis of the human mind working with anthropologists, philosophers, psychologists, and cognitive scientists. The rapidly developing fields of social and cultural neuroscience (Han and Northoff, 2008; Chiao and Ambady, 2007; Lieberman, 2007; Frith, 2008) open new research avenues, offer new sources of evidence, and raise a number of issues that demand archaeological attention and carry the promise for productive cooperation between archaeology and neuroscience. "Neuroarchaeology" is essentially a systematic attempt to channel this huge emerging potential in the direction of a common integrated research program targeting the big picture of human mind and its development in human evolution (both before and most importantly after the so-called speciation phase) (Malafouris and Renfrew, 2008; Renfrew et al., 2009). At a theoretical level, neuroarchaeology is

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grounded upon the Material Engagement approach to the study of mind (Malafouris, 2004, 2008a; Renfrew, 2004). At a methodological level, neuroarchaeology aims *at bridging the gap between neural and cultural plasticity* by putting material culture, embodiment, time and long term change at center stage in the study of mind (Malafouris, 2008a; Malafouris and Renfrew, 2008).

One could identify three general objectives as the differentiation feature of the approach we call "neuroarchaeology." These are:

(a) To incorporate, contextualize, and translate, in a scale that matters to cognitive archaeology, key recent developments in neuroscience (cognitive, social, affective, and cultural).
(b) To promote and stimulate a systematic and critical reflection on neuroscience's claims on the basis of our current archaeological knowledge about the biocultural origins and evolution of human mind.

And finally,

(c) To provide a platform for active and informed cross-disciplinary dialogue among archaeology, anthropology, and neuroscience.

It is hoped that pursue of the above objectives will enable and stimulate new synergies to emerge between archaeology and neuroscience. Synergies, that could provide a new means for exploring the unity and diversity of the human mind and maybe help us articulate and address the new challenging research questions that are constantly emerging at the interface between brain and culture.

Foundational issues: theoretical and methodological challenges

The general analytic objectives of neuroarchaeology remain the same with that of cognitive archaeology in the broader sense: That is, to use the material remains of the past in order to understand past *ways of thinking* as they emerge and take shape in different evolutionary and cultural trajectories (see Renfrew, 1994). Developing a neuroarchaeology of mind we can hope to learn much more about the remarkable plasticity of mind by exploring the neuroscientific basis for learning and for the development of material culture. The key challenge for neuroarchaeology in this context lies in figuring out how our plastic enculturated brains and bodies should be understood within the wider extended networks of non-biological props and scaffolds that delineate the real spatial and temporal boundaries of the human cognitive map (Malafouris, 2008b; Malafouris and Renfrew, 2008).

Naturally, special emphasis is now placed on the changing human brain. But, it is important to note, that this empirical opening of neuroarchaeology into the biological bases of the human mind does not aim to reduce cultural change, difference, and variability to some innate biological universals. The aim is rather to understand the nature and meaning of cultural difference and variation across the different levels and temporal scales of human experience and explain how the one affects, interacts, and explains the other in evolutionary time. Thus although neuroarchaeology, as a research paradigm, may seem to resemble that of evolutionary psychology (see review by Cosmides and Toody, 1987) the two projects in fact share very little in terms of theoretical presuppositions. The perspective of "neuroarchaeology" advanced here does not subscribe either to the "modular" or "Pleistocene" thesis used by classical evolutionary psychology to describe the structure of the human cognition. This "maladaptationist" (see Dupré, 2008) view of human cognitive evolution as fixed in the Stone Age has been recently criticized on several grounds. For instance, recent advances in genomics demand that we abandon a number of well-entrenched ideas, for instance, the view of the genome as some kind of blueprint for the production of an organism. A new more complex picture of the genome is gradually emerging opening up a wide range of possibilities for thinking about the evolutionary process. New theoretical frameworks such as that of "neuroconstructivism" (Mareschal et al., 2007a, b; Westermann et al., 2007; Quartz and Sejnowski, 1997) and "probabilistic epigenesis" (Gottlieb, 2003, 2007) provide us a new, non-linear, and interactive model for understanding the relationship between genes, the brain, and behavior that characterize human cognitive becoming. In particular, cognitive development is no longer seen as the progressive unfolding of information that is laid out in the genome. The traditional view of a one-directional flow of cause and effect from genes (DNA) to RNA to the structure of proteins they encode gives way to a subtler picture where *physical, social, cultural aspects of environment* and behavior play fundamental role in triggering the expression of genes.

Although some basic genetic substratum certainly exists as the product of human speciation process, there is now increasingly accumulated evidence for the "ongoing evolution" scenario (Dupré, 2008; Evans et al., 2005; Mithen and Parsons, 2008). So far as human mind and its operation is concerned, one can hardly find any universal truths with real explanatory power. Although recent DNA studies may well demonstrate that for at least 100,000 years now the majority of the human genome is conserved with only minor variations across human cultures, it nonetheless tell us very little about the actual nature of human cognition. In fact, as archaeology may well testify, significant parts and episodes of the story of mind appear relatively recently in the archaeological record and can certainly be seen as the emergent products of various cultural trajectories, rather than innate biological capacities. If there is something distinctive about human psychology is the extraordinary projective plasticity of mind and its openness to cultural influence and variation. The hallmark of human cognitive evolution may not be based on the ever-increasing sophistication or specialization of a modular mind, but upon an ever-increasing representational flexibility that allows for environmentally and culturally derived plastic changes in the structure and functional architecture of the human brain. This co-evolutionary process of deep enculturation, material engagement (Malafouris, 2004, 2008a, b), and "profound embodiment" (Clark, 2008; Wheeler and Clark, 2008; Chiel and Beer, 1997) started some 2.6 million years ago with the construction of the first stone tools (Stout et al., 2008; Stout and Chaminade, 2007) and continues into the present. It is this process that occupies the principal focus for neuroarchaeology as a project primarily pre-occupied with explaining change and understanding the long-term developmental mechanisms by which the bidirectional, mutual constitution of brain and culture occurs. Thus, neuroarchaeology can be seen as the cultural neuroscience of the past. In a way, both disciplines share the common objective, albeit pursued on a different spatial and temporal scale: "to investigate and characterize the mechanisms by which this hypothesized bidirectional, mutual constitution of culture, brain, and genes occurs" (Chiao and Ambady, p. 238). Most importantly, they try to accomplish the above without replacing "the language of culture with the language of neurons or molecules" (Chiao and Ambady, 2007, p. 239).

Establishing empirical, but also culturally sensitive and philosophically informed, links between brain's functional structure, and archaeologically observable behaviors is thus a central challenge in the development of neuroarchaeology. This calls for a methodology that, among other things, must be able to integrate different temporalities (cultural, evolutionary, and neuronal). Only then we can start thinking about the possible ways that, for instance, in our previous example of tool use, a brain activation map and a *chaîne opératoire* (Schlanger, 1994; Bar-Yosef and Van Peer, 2009) can be combined and complement each other. A precondition for such an understanding however, is to recognize that "a cognitive process is delimited by the functional relationships among the elements that participate in it, rather than by the spatial collocation of the elements" (Hollan et al., 2000, p. 176). Although the allure of a brain scan may seem more convincing an evidence for the active human mind than the stratigraphic section of the Blombos cave, it is only so because of our deeply entrenched conviction about what counts as thinking and about where one should be looking for its material traces. From a long-term archaeological cross-cultural perspective, I suggest, it would be more productive, to explore the assumption that human intelligence "spreads out" beyond the skin into culture and the material world (cf. Knappett, 2006; Gosden, 2008). Equally important is to allow archaeology to inform and influence the questions to be asked in the environment of the brain (MRI) scanner.

Following the above crucial theoretical points we have also the issue of the methods of neuroarchaeology. Obviously, archaeology has no direct access to the human brain. Nonetheless, the use of functional MRI has the potential to play a prominent role in neuroarchaeology as part of experimental studies with modern humans. A series of neuroimaging studies conducted in the last few years by D. Stout and his colleagues paved the way in this direction and have successfully met some of the challenges involved. In particular, conducting a series of imaging experiments using positron emission tomography (PET), Stout and Chaminade (2007, 2009) compared previously inexperienced subjects making simple, so-called Oldowan, stone tools both before and after completing four weekly practice sessions in stone tool manufacture. The observed functional changes in brain activation patterns following the practice sessions, that is cultural activity**,** offered some good indications of how the possible causal linkages and correlations between the changing lithic technologies and the functional anatomy of the brain can be understood in their evolutionary context (Stout and Chaminade, 2007; Stout, 2005; Stout et al., 2008).

So, what are we to make out of this study? Clearly there are many problems — not the least because of the constraints imposed by using functional imaging — but there is also a great deal of promise, especially if one considers that brain imaging itself is in a very active state of constant development. As archaeologists we doubt that simply knowing which area of the brain lights up during the performance of some cultural task, like knapping for example, is the sort of information that will make the big difference in the study of human cognition. No measurement in regional brain activity tells you, in itself, the most important part of the story about the cognitive task in question. There is, nonetheless, one thing for which neuroscience merits full recognition and I suggest it is upon this point that neuroarchaeology and cultural neuroscience need to capitalize. The neuroimage has demystified representations. It has placed the perennial question of "how 'reality out there' represented in our heads?" under a new light and has given us some good indications that this might be the wrong question to ask after all. No doubt the enchanting power of the neuroimage may still, quite often, be pointing to the wrong "neurocentric" direction, as far as the topology of human cognition is concerned, but it can nonetheless help us avoid most of the classical representational fallacies and dualistic pitfalls that has been around for too long and still inform a good deal of thinking in philosophy, archaeology, and anthropology of mind. Thus neuroimaging can be a powerful tool in the study of cultural cognition as long as it remains clear that (a) cognitive processes and associated neural systems engaged in a complex natural situation may differ substantially from those observed in the purified environment of the lab (cf. Kingstone et al., 2008) and (b) that there might well be "external" components with a constitutive role for the enactment of a given cognitive operation that do not correlate to any observed brain activation pattern or evoked BOLD response simply because they do not participate in brain's *space* or *time*.

Steps to a "neuroarchaeology of mind": bridging the gap between neural and cultural plasticity

No doubt these exciting prospects, leave us with the important epistemological challenge of developing common relational ways of thinking about the complex interactions between brain–body–world (see also Gosden, 2008; Jordan, 2008; Sutton, 2008).

Thus in this final part of my paper I will attempt to articulate some of the questions and problems which can be seen as emerging at the cross-section between neuroarchaeology and cultural neuroscience, and postulate some concrete proposals on the ways in which these issues might be addressed in future collaborative research.

We should start pointing out that explaining cognitive variation is inseparable from the study of how cultural differences came into being which entails close examination of the way cultural phenomena, physical artifacts, and practices were created, transformed, and transmitted across the scales of time.

Cognitive and developmental neuroscience have already made important contributions in advancing our knowledge about neural plasticity and the constant experiential, social, and cultural modulation of the developing human brain. Cultural neuroscience could help archaeologists learn more about the biological and neural substrates of human cognition in a cultural context and thus to identify and better define their archaeologically visible attributes. Key questions and prevailing assumptions about the emergence of modern humans and the origins of symbol, language, self-awareness, and explicit representational thinking can be critically reviewed in the light of recent neuroscientific findings and archaeological findings.

Similarly, from their own distinctive perspective, archaeology and anthropology offer a wealth of concrete examples and case studies on the variability and plasticity of human cultural cognition. New empirical findings and current controversies in the archaeology of mind can be seen to challenge our conventional understanding of the relationship between biology and culture. Archaeological data can be used to constrain models of human cognitive evolution and illustrate how significant cognitive changes are the product of engagement processes between people and the material world realized in different trajectories of cultural development.

It can be argued that the most interesting information that might come from the merging of cultural neuroscience, archaeology, and anthropology would be comparative. That is, the ability to detect similarities and differences between different contexts in respect to the neural, behavioral, and cultural correlates of specific developmental aspects of human cognition. It is essential for the future of cultural neuroscience research in this area that the fine-grained ethnographic description about the cultural variation of human individual, combined with insights from cognitive archaeology and philosophy of mind should be allowed to influence the nature of questions to be pursued and hypotheses to be explored.

To this end, the unique preoccupation of archaeology with material culture, change, long time-spans, and large-scale processes can provide an additional means for exploring the emergence of cultural variation. New forms of engagement with the material world bring about new cognitive, social, and affective possibilities and constraints for the human brain. New styles, materials, manufacture techniques, and cultural practices would put novel demands on the bodies and brains of people making and using those objects. Thus, focusing on the effect that the development of new materials and technologies, from the tools of the Stone Age to the more recent "exographic" technologies and cultural practices (e.g., uses of space and conceptions of time), as these can be observed in the archaeological record, might be our key to understand how culture shapes the brain.

Take for instance the example of a Mycenaean Linear B tablet (Malafouris, 2004, in press). This object did much more to the Mycenaean mind than simply enabling the displacement — what we may call extended *redistribution* — of the mnemonic operational sequence of acquisition–storage–retrieval outside the biological boundaries of the brain. The Linear B tablets more than simply amplifying the Mycenaean memory system they brought about a radical change into the nature of the cognitive operations involved and in the functional architecture of the system as a whole. They have effected an *extended reorganization*. More simply, the Mycenaean person now engages in a different sort of cognitive behavior; a new cognitive operation, that is reading, now emerges and becomes available in the system (for the possible neurological implications of that see Castro-Caldas et al., 1998). Moreover, the decrease of brain activity in the working memory system that the use of the Linear B tablets have brought about can be associated with an increase to the overall multitasking ability of the cognitive system (Ramsey et al., 2004). Increased and skilful material engagement often correlates with neuronal disengagement which effects a liberation of processing resources (e.g., Gilbert et al., 2001) and facilitates "neural recycling" (Dehaene, 2005).

A joint attempt at reconstructing the emergence of this embodied and interactive system in human evolution and its cultural variation could foster a two-way productive dialogue between cultural neuroscience and archaeology (see also Jordan, 2008; Sutton, 2008). The task that confront us is about bringing these two perspectives together and integrating their insights and ways of thinking, avoiding reducing the one to the other.

Neuroarchaeology, in order to avoid falling into the trap of neurocentrism, is committed to an interactionist, rather than reductionsit view of mind and brain. Such a view will help us meet the epistemological challenge of developing common relational ways of interpreting the complex interactions between brain–body–world. Thus my contention is that the project of neuroarchaeology should be grounded on the general framework of Material Engagement Theory (MET) (Malafouris, 2004, 2007, 2008a; Renfrew, 2004, 2006, 2007). The distinctive features of this new approach to the archaeology of mind that draws upon the paradigms of distributed and extended mind (Hutchins, 1995, 2008; Clark, 1997) can be briefly summarized by way of two major premises: First MET is systematically concerned with figuring out the causal efficacy of the materiality and the built environment in the human cognitive system [this I call following Wheeler (forthcoming) the element of "vital materiality."] The second relates to the expansion of the unit of analysis beyond the boundaries of the individual brain in order to incorporate body and culture. The key idea here is very similar to that which can be found at the heart of the Distributed Cognition approach and it is nicely expressed by Edwin Hutchins in the following quote:

> [A] good deal of contemporary thinking, and probably an even greater proportion of ancient thinking, happens in *interaction* of brain and body with the world. This seems innocent enough and many people take it to mean simply that thinking is something that happens in the brain as a consequence of interaction with the world. That is not the claim being made here. The claim here is that, first and foremost, thinking *is* interactions of brain and body with the world. Those interactions are not evidence of, or reflections of, underlying thought processes. They are instead the thinking processes themselves (Hutchins, 2008, p. 2112).

Some concluding thoughts

In this paper I have reviewed in brief some recent empirical and theoretical developments in the archaeology of mind and tried to articulate some of the possible questions and approaches that can be seen as emerging at the interface between brain and culture over the long-term of human becoming. Against this background I sketched the possible role that neuroarchaeology can play in the development of cultural neuroscience and outlined some of the foundational issues and methodological challenges such a project might face. Although the emphasis of neuroarchaeology falls naturally on the changing human brain and its long-term evolutionary and developmental trajectories I suggested that we should constantly remind ourselves, that this is a brain inextricably tied with a body and firmly situated in culture and the material world. A basic commitment to the constitutive intertwining of brain with culture is necessary in order to avoid falling into the trap of neurocentrism which can easily lead us to mistake the properties of culture for the properties of the individual brain. Although the complexity of causal paths from brain to culture and from culture to brain can make the project of neuroarchaeology seem difficult at times, there is a great deal of promise. Approaching the human brain as a cultural artifact (see also Mithen and Parsons, 2008) and using the brain–artifact interface (BAI) as the key unit of analysis (Malafouris, 2008a) may offer a much needed bridge between neural and cultural plasticity.

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CHAPTER 19

Cultural neuroscience and psychopathology: prospects for cultural psychiatry

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Abstract: There is a long tradition that seeks to understand the impact of culture on the causes, form, treatment, and outcome of psychiatric disorders. An early, colonialist literature attributed cultural characteristics and variations in psychopathology and behavior to deficiencies in the brains of colonized peoples. Contemporary research in social and cultural neuroscience holds the promise of moving beyond these invidious comparisons to a more sophisticated understanding of cultural variations in brain function relevant to psychiatry. To achieve this, however, we need better models of the nature of psychopathology and of culture itself. Culture is not simply a set of traits or characteristics shared by people with a common geographic, historical, or ethnic background. Current anthropology understands culture as fluid, flexible systems of discourse, institutions, and practices, which individuals actively use for self-fashioning and social positioning. Globalization introduces new cultural dynamics and demands that we rethink culture in relation to a wider domain of evolving identities, knowledge, and practice. Psychopathology is not reducible to brain dysfunction in either its causes, mechanisms, or expression. In addition to neuropsychiatric disorders, the problems that people bring to psychiatrists may result from disorders in cognition, the personal and social meanings of experience, and the dynamics of interpersonal interactions or social systems and institutions. The shifting meanings of culture and psychopathology have implications for efforts to apply cultural neuroscience to psychiatry. We consider how cultural neuroscience can refine use of culture and its role in psychopathology using the example of adolescent aggression as a symptom of conduct disorder.

Keywords: culture; psychiatry; neuroscience; diversity; ethnicity; racism; research methodology

Introduction

Cultural psychiatry is concerned with variations in mental health and illness across diverse societies, communities, and groups. This diversity is a challenge for theories of psychopathology as well as for the provision of effective mental health services and interventions. While biology and psychology have assumed a basic universality of human constitution and experience, both fields have generated ample evidence of wide cultural variations among human groups. A parallel body of work demonstrates the diversity of forms of

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psychopathology and of corresponding methods of coping and healing. In a world facing growing diversity through migration, intermixing, and creative exchanges through mass media, culture has become a key issue in our understanding of mental health and illness. Cultural neuroscience holds the prospect of advancing psychiatric science and practice through models that recognize the essential interactions of culture and biology and that go beyond this dialectic to formulate a cultural biology. At the same time, cultural critique offers a corrective to our current practices by showing some of the social determinants and conceptual limitations of current models that reflect their cultural, historical, and political origins and purposes.

Comprehensive explanatory models for psychopathology require the integration of multiple perspectives including genetics, neurobiology, cognitive mechanisms, and sociocultural frameworks. While scientific research into the etiology of psychiatric disorders, particularly since the "Decade of the Brain," has channeled most of its efforts to the study of biological explanations, the same studies that document genetic and constitutional bases for psychiatric disorders have provided evidence for the importance of environmental, familial, social, and cultural contexts in the causes and course of psychopathology (Kendler, 2008). Psychiatric researchers have embraced the new methodologies of genomics and neuroimaging as a basis for understanding the causes of psychopathology and devising effective treatments. For example, it has recently been suggested that the identification of the dysfunction of specific brain circuits associated with symptoms of mental disorders can make an important contribution to a new scientifically grounded psychiatric nosology (Hyman, 2007). Methodological advances in neuroimaging and imaging genomics have opened up possibilities for studying the biological bases of individual differences in illness experience and cognition, raising the prospect of developing individually tailored clinical interventions (McGowan et al., 2009; Plomin et al., 2002; Ronald et al., 2005; Rutter et al., 1999). The implication is that the fault lines that define discrete disorders or dimensions of psychopathology can be found in the brain. However, psychopathology is not merely a question of distinctive genetic and neural signatures but of lived experience, developmental histories, dynamic interactions, and cultural contexts (Henningsen and Kirmayer, 2000). The problems that patients bring to clinicians often include social predicaments that require corresponding conceptual frameworks to guide assessment and intervention (Gone and Kirmayer, in press; Kirmayer, 2005).

The rapid growth of neuroimaging approaches to the study of the mind in the last two decades has given rise to new subfields, such as affective and social neuroscience, concerned with mapping mental states, emotions, personality, and dispositions onto the brain. Findings from neuroscience can illuminate the neurobiological correlates of psychopathology and are frequently invoked in theories of autism, schizophrenia, depression, attention deficit hyperactivity disorder (ADHD), and antisocial personality disorder (ASPD). These technologies also provide new ways of distinguishing groups of people based on gender, age, language, and other dimensions of social identity in terms of structural or functional differences in neural processing. Very recently, cognitive neuroscientists have turned to the subject of cultural difference and have begun to investigate how culture interacts with the neural mechanisms associated with social, emotional, attentional, and perceptual processes. If cultural variations in the symptoms of psychiatric disorders are reflected in structural and functional differences in the brain, then data from cultural neuroscience might be used in diagnostic assessment (Han and Northoff, 2008).

Although, to our knowledge, data from cultural neuroscience have not yet been applied to explaining cultural differences in psychopathology, cultural neuroscience eventually may allow us to address a wide range of questions of interest to psychiatry, including: How can we account for socially and culturally patterned differences in vulnerability to psychiatric disorders? What processes mediate the negative effects of racial discrimination, prejudice, and microaggression on health? How do culturally mediated developmental experiences influence subsequent emotion regulation and expression? How do cultural differences in self-construal interact with mood regulation to modulate vulnerability to depression? How do cultural styles of expressing distress influence symptom experience? How do psychopharmacological agents differentially affect the brains of people with different culturally-based developmental experiences or current life circumstances? How do placebos, psychotherapy, and other psychosocial and symbolic interventions exert their effects on cognition, emotion, physiology, and behavior? (Alarcón et al., 2002; Kirmayer, 2006).

Current approaches in cultural neuroscience however pose a number of potential problems for psychiatry, unless experimental paradigms and conceptual frameworks are developed that attend to the social contexts of the participants in research and the underlying assumptions that guide the design and interpretation of studies (Choudhury et al., 2009). Without attention to these issues including consideration of the changing concepts of culture, efforts to locate cultural differences in the brain risk naturalizing social differences and reifying subtle forms of discrimination.

In this article, we consider some challenges and possible directions for a cultural neuroscience that may yield useful insights for psychiatry. Cultural neuroscience can add crucial dimensions to the project for a scientific psychiatry by clarifying how specific social and cultural experiences influence the brain in health and illness. To make a useful contribution to psychiatry, however, cultural neuroscience needs careful rethinking of the ways that it conceptualizes both culture and psychopathology. We begin by reviewing some recent findings from ''transcultural neuroimaging'' studies of various cognitive processes to illustrate some of the dilemmas raised by current studies in cultural neuroscience. Second, by sketching a brief history of cultural psychiatry, we illustrate the risks of reifying culture in the brain and emphasize the need for more nuanced approaches to culture in experimental paradigms. Third, we outline an approach to the role of culture in psychopathology that integrates recent findings from neuroscience and genetics about the bidirectional interactions between brain and environment with the shifting meanings of culture itself in a world increasingly woven together by the forces of globalization. Finally, we use the example of adolescent psychopathology — in particular, the symptom of aggression in conduct disorder (CD) — to explore how cultural neuroscience can clarify the brain's role in cross-cultural differences in psychopathology by expanding its analysis beyond the individual brain to include social and cultural contexts.

Scanning ''culture'' and generating identities

Until recently, mainstream psychology held to the view that basic cognitive processes are universal. However, research in psychology during the last decade has demonstrated that attentional, inferential, and learning processes differ markedly among adults in different cultures (Nisbett, 2007; Nisbett and Miyamoto, 2005). This work implies that culture is inscribed in the brain through developmental processes so that individuals approach new tasks or social situations with particular cognitive styles or strategies. These studies also show that while there is considerable individual variation within groups, substantial and consistent between group differences can be identified.

In recent years, a new genre of functional neuroimaging (fMRI) studies has been recasting cultural identity in terms of differential neural activation patterns involved in performance on various tasks, using ''culture'' as an experimental variable (see Han and Northoff, 2008). This approach conceives of both cognitive functions and cultural differences as processes that can be located in the brain. Current designs for neuroimaging experiments require neat divisions of subjects into discrete groups to produce comparisons, and usually employ simple proxies for culture and ethnicity. For example, one fMRI study comparing Western and East Asian participants found an interaction between cultural group and the level of frontoparietal activity during context-dependent versus context-independent judgment tasks, suggesting that modulation of an attentional network in the brain may parallel findings from social psychological studies that show differential attention to context and stimulus across cultural groups (Hedden et al., 2008). Similarly, distinctions in cortical activation and connectivity between Chinese and English speakers have been demonstrated in tasks tapping reading skills (Qiu et al., 2008), as well as arithmetic (Tang et al., 2006) and musical phrase processing (Nan et al., 2008).

Several recent studies suggest that culture also modulates functional activation of the brain areas involved in social cognition (Chiao et al., in press, 2008; Kobayashi et al., 2007; Molnar-Szakacs et al., 2007; Zhang et al., 2006; Zhu et al., 2007). For example, a comparison between processing of information about self and other in Chinese and Western participants using fMRI demonstrated differential patterns of recruitment of the medial prefrontal cortex (MPFC). For the Chinese, processing of information about self and a closely related other involved similar patterns of activation, while Westerners showed greater difference in pattern of processing for self and other. These differences were attributed to cultural differences in self-representation (Zhu et al., 2007). The differential pattern of neural activation was thought to reflect the distinct cognitive processes associated with an emphasis on greater interpersonal connectedness in Chinese cultures compared with a greater emphasis on the development of the individual self in Western cultures. Similarly, neural activity within the anterior rostral portion of MPFC during processing of self judgments has been shown to predict the degree to which people across cultures construe their sense of self as either individualistic or collectivistic (Chiao et al., 2008).

These fMRI studies indicate that culture shapes not only neural representations of the self, but also the understanding of others in same- or other-culture groups. For example, higher performance on a social cognition task, the ‘‘Reading the Mind in the Eyes’’ task (Baron-Cohen et al., 2001), was found to be correlated with ‘‘culturally tuned’’ patterns of neural activation in posterior superior temporal sulcus in Japanese and US Caucasian participants when either group was engaged in decoding the mental state of members of same culture versus other cultures in photographic stimuli (Adams et al., 2009).

While these data indicate that neural mechanisms subserving several cognitive processes are modulated by some aspects of culture, important methodological and conceptual questions remain. In their review of transcultural neuroimaging studies, Han and Northoff (2008) raise a number of problems with respect to the interpretation of these neural differences. For example, to what extent are these differences across cultural groups due to differences in task-solving strategies, neuroanatomical structure, or the conceptual meaning of the task? Most experimental tasks are not culture-free but depend on cultural background knowledge, and are interpreted and approached in terms of previous culturally mediated experiences. Thus, apparent cultural differences in neural processing may reflect different ways of responding to the demand characteristics of the setting or preferential use of specific cognitive strategies rather than revealing any fixed characteristics of a group.

The most fundamental issue, however, concerns the very notion of ‘‘culture,’’ which is employed in these experiments to construct distinct experimental groups. In the studies reviewed above, culture is conflated with individual identity, and painted with a broad brush, grouping individuals together as ‘‘Chinese,’’ ‘‘Western,’’ ‘‘Caucasian,’’ and other geographic, ethnic, or racialized labels. These labels have complex histories and current meanings and certainly do not identify homogeneous groups (leaving aside the fact that most studies are conducted with college student subjects who are not representative of the social, economic, and cultural diversity of their societies or ethnic groups). Nevertheless, these fMRI studies compare groups, usually consisting of from 8 to 15 participants, each of whom is taken to represent a particular cultural identity. While the constraints of fMRI as an experimental paradigm are increasingly recognized, the ways in which ethnocultural groups are constructed also demand critical reflection. Unpacking the notions of culture, race and ethnicity is essential to advance cultural neuroscience to avoid reproducing stereotypes in ways that may have profoundly damaging effects in the wider society. Before we discuss a more reflexive approach to culture, we describe how problematic the use of ethnoracial categories can be, using historical examples from colonial psychiatry.

Essentializing culture in the brain

Although culture, in the ecological sense of the humanly constructed environment and its associated way of life, is basic to the experience of everyone everywhere, in psychiatric research and practice, culture is usually conflated with ethnicity, race, and other social categories. These categories are not "natural kinds" found in the world but socially constructed distinctions that mark off groups of people in ways that essentialize their identities and that often serve to justify systems of exploitation and oppression. Indeed, there is an older tradition of such thinking in psychiatry that, to a modern eye, looks plainly racist. Several generations of colonial psychiatrists and their colleagues made claims about the inferior brains of colonized peoples to explain their primitive, childish, and pathological behavior (Kirmayer, 2007b).

Emil Kraepelin (1856–1926), one of the founders of modern psychiatry, undertook a voyage to Java in 1903 to address questions about the universality of psychopathology. He found not only similarities but also differences in the symptoms of patients in Java compared to those in Germany, which he interpreted as evidence of more primitive psychological development of the Javanese (Kraepelin, 1904). In later work, he explained other such social and cultural differences in biological terms as indications of degeneration of the nervous system due to the use of alcohol, syphilis, or heredity (Roelcke, 1997). Ultimately, Kraepelin supported notions of racial hygiene that were appropriated by the Nazi ideology that justified the murder of millions.

The French colonial psychiatrist Antoine Porot (1876–1965), architect of most of the mental health programs in North Africa in the first half of the last century, argued that the native Algerian mind was structurally different from that of the civilized European (Porot, 1918; Keller, 2007). The native was held to have less developed cortical activity and his behavior was therefore driven by activity of the "primitive brain" of the diencephalon. This resulted in behavior that Porot described as more impulsive, childish, suggestible, and dominated by emotion. Such images of North African people rationalized their domination by French colonial institutions. Similarly, the British colonial psychiatrist J.C. Carothers (1903–1989) who worked in East Africa, described Africans as developmentally child-like owing to their underdeveloped frontal lobes, which resulted in the functional equivalent of a leucotomy (Carothers, 1954; McCulloch, 1995). This accounted for what Carothers assumed to be a low prevalence of depression in Africa and for the relative lack of feelings of guilt among those with depression — an impression that was eventually refuted by epidemiological research (Orley and Wing, 1979).

At the heart of this colonial comparative psychiatry was the use of a racial typology and a hierarchy of people, with Europeans at the top (Lock, 1993). Northern European male norms and values provided implicit standards for normal and abnormal behavior in mental health and illness (Gaines, 1992). These norms could be invoked not as the biological characteristics of a people but as achievements of a uniquely advanced and morally superior civilization and gender. However, attributing cultural difference to the brain made it intrinsic to the physical make-up of people, sidestepping the need to defend a historically contingent hierarchy of values, and ultimately serving explicitly racist ideologies.[1]

The views of colonized people as child-like, impulsive, and lacking the reason and restraint characteristic of civilized men were echoed in psychoanalytically inspired writings (Mannoni, 1990), showing that biological theory was not

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[1] Of course, this sort of crude biological essentialism need not serve only racist or colonialist ideas. The Japanese neuropsychologist Tadanobu Tsunoda promoted the idea that Japanese have unique brains owing to the nature of their language (Tsunoda, 1985).

necessary to establish this hierarchy. It is equally possible to rationalize such stereotypes and racist ideologies on the basis of psychological theory (Jahoda, 1999; Lucas and Barrett, 1995; Waldram, 2004). Psychological essentialism is a common cognitive habit and readily leads to the production of stereotypes and the construction of human groups as discrete entities (Bastian and Haslam, 2007). This style of thought works hand in hand with the categorical thinking of psychiatric nosology so that the ‘‘essence’’ of a group is conflated with the ‘‘essence’’ of a specific form of psychopathology.

Although a growing body of evidence shows how culture shapes the brain, we do not want to revisit these dark chapters in psychiatric history. The slippery slope begins with biologizing social facts like collective identity, and with the focus on a biologically or racially construed ‘‘people’’ in place of the diversity the variety of individuals' experiences. Common to all of these tendentious uses of biology is a lack of systematic attention to and respect for the power and consequences of social and political arrangements, which not only shape experience and determine how we configure human difference but also influence how we think about and study the brain. Hence, the need for a critical cultural neuroscience that acknowledges the powerful interests and agendas behind the activities of psychiatric research and its clinical applications.

Locating culture in the social world

In much of the work on culture and psychiatry, old and new, there are recurrent confusions about the constructs of culture, ethnicity, race, and biological (phenotypic and genetic) variation. Sorting this out is crucial for thinking clearly about cultural neuroscience and its potential role in psychiatry. While anthropologists have developed rich and multilayered meanings of culture, neuroscientists have tended to reduce culture to discrete categories and components, associating it with group membership, or parsing it into measurable traits. Neuroscience studies have tended to equate culture with nation-state or geographic region, uncritically adopt racial categories, or make comparisons between groups as broad as ‘‘Western and Asian.’’ In this section, we provide a closer reading of the constructions of these concepts and their differences to encourage more careful definitions of ‘‘groups’’ and cultural variables in brain research.

Anthropologists have engaged in a long debate about how best to conceptualize culture (Kuper, 1999). Culture generally includes all of the material and non-tangible aspects of life that a person holds in common with other individuals forming a social group, encompassing social institutions (e.g., family, community, or religion), knowledge (languages, skills, conceptual models and frameworks), attitudes (moral and esthetic values and orientations toward self and others) and practices (child-rearing styles, family interactions, etiquette, daily rituals and routines, as well as special ceremonies for changes in social role or status). Cultures are not, however, static, bounded entities that denote homogeneity and internal cohesion within groups. Rather, cultures are dynamic, permeable, and changeable systems, with internal tensions and contradictions, which individuals actively use for self-fashioning and social positioning. As a result, in the contemporary world, most individuals participate in multiple cultural systems or streams of influence and show ways of thinking, perceiving, and acting derived from these multiple systems depending on their goals, their relationships with others, the social setting, and their social status or position.

Given this dynamic complexity of culture, cultural neuroscience must go beyond using group identity as a proxy to measure specific characteristics relevant to the process of interest. Insights from anthropology can provide alternative approaches to culture that are more meaningful than ethnic or racial labels, yet also operationalizable and measurable. Focusing attention on identifying measurable domains of culture such as family interaction, gender, religion, diet, or concepts of personhood can free cultural neuroscience to look beyond ethnicities to investigate the particularities of culture within participants' ways of life. The aim is to identify culture-related cognitions, attitudes, and behaviors that correlate with processes relevant to understanding psychopathology.

Most of these culture-related cognitions, attitudes, and behaviors will not be unique to any one culture but shared to varying degrees by people across different racial or ethnic categories. This reflects the individual diversity within any culture, which is increasing in response to the forces of globalization. The mixing of cultures brought about by increased mobility, telecommunications, and mass media has resulted in hybrid identities, and global subcultures stratified not by race or ethnicity but by age, education, occupation, and other types of social status (Hannerz, 1992; Kraidy, 2005; Niezen, 2004). Recognizing the internal diversity of cultural groups and the impact of globalization on cultures that were once relatively isolated should lead to caution in attaching specific traits or characteristics to any individual on the basis of their cultural background or ethnicity. Instead, we need to verify the presence of specific culture-related variables in each individual directly.

The same methodology that identifies differences between cultural groups can capture some of the individual variation within a cultural group. This is well illustrated by a recent fMRI study investigating the neural basis of individualist versus collectivist self-concepts, which compared neural activation patterns of Japanese and American participants in a self-description task. As expected, individualistic and collectivistic self-concepts were related to different patterns of brain activation; however, modes of self-construal were not well predicted by ethnic affiliation (Chiao et al., in press). While activity in all participants in MPFC was modulated as a function of self-construal style, the Japanese and American groups could not be distinguished by neural representations of collectivist and individualist self-construal, respectively. In fact, a comparable number of individuals in each group endorsed collectivist and individualist concepts of self. Focusing on ethnicity alone would have yielded no difference, while measuring the cultural orientation revealed a strong correlation between modes of self-construal and pattern of brain activation. Clearly, categories such as ethnic affiliation may group together people who do not all share important cultural variables, and divide people who share much. Moreover, the same study demonstrated that priming bicultural individuals with either individualistic or collectivistic values predicted the activation of MPFC and posterior cingulate cortex, suggesting that these neural representations of self-concept are not entirely fixed traits or characteristics of individuals but dynamic cognitive strategies influenced by set and context (Chiao et al., in press). This study illustrates the value for experimental studies of unpacking cultural identity to measure cognitive mediators of cultural difference and of manipulating instructions, social expectations, or social context to clarify the interaction of cultural background with individual differences and performance.

Concepts and categories of culture, race, and ethnicity depend on social and historical context. In the United States, for example, ethnic, geographic, racial, and linguistic distinctions that reflect the complex history of migration were simplified and consolidated in census categories that created five ethnoracial blocs: African American, American Indian and Alaska Native, Asian American and Pacific Islander, Hispanic, and White (Hollinger, 1995). The vast majority of psychiatric research in the United States on ‘‘culture’’ as well as training materials and clinical guidelines in mental health has used these categories which however politically important they have come to be, thoroughly confound and conflate geographic origin, language, ethnicity, racial ideology, and cultural difference.

Racial categories are constructed on the basis of differences (often but not necessarily visual differences) that are made salient by being socially marked and distinguished. Racial distinctions are built on the propensity we have to form categories of humans that constitute in-groups and out-groups, but many characteristics can be attached to this division of people into *us* and *them*, which then appears natural or given (Cosmides et al., 2003; Hirschfeld, 1996). These categories lend themselves to elaborating a racial ideology that rationalizes and legitimates regimes of domination, violence and exploitation (Fredrickson, 2002). While we may be biologically prepared to make such categorical distinctions, the specific differences we mark, the attributions we make, and their consequences are all socially determined.

Similar arguments can be made about our notions of ethnicity (Banks, 1996; Modood, 2007; Phillips, 2007). Like race, ethnicity is always defined vis-à-vis others who are viewed as different and used to define who does and does not belong to an ''in-group'' or an ''out-group.'' However, while race tends to be ascribed to a group by others and viewed as an intrinsic, biological characteristic, ethnicity is more often self-ascribed, and defined in terms of shared origins, history, and traditions. As such, ethnicity may have more explicit links to conscious agency, choice, and self-fashioning but it remains a short segue from ethnic identity as belonging to a group or community with a shared history to essentialized notions of ethnicity as ''blood,'' lineage, and purity. The same essentializing can occur with religious identity.

Attempts to ground racial concepts in biology founder on the low correlation between the social markers of racial difference and any underlying genetic basis for phenotypic differences. There are circumstances in which knowing the person's racial identity (whether self-ascribed or attached to them by the institutions of a dominant society or group) may be useful clinically for calculating the likelihood of specific patterns of illness behavior, help-seeking, the presence and course of particular disorders, and treatment responses (e.g., Braun et al., 2007; Malat and Hamilton, 2006; Smedley et al., 2003). However, race is useful mainly as a marker of potential exposure to racism and discrimination, which have direct effects on health as well as access to health services (Le Cook et al., 2009; Noh et al., 2007). All of these effects depend on the social meanings of race for a specific population in a particular cultural context at a particular moment in time. New migration, intermarriage, phenotypic changes, and new social conventions of labeling can change the meaning of a racial category and its correlation with other biological or psychological variables. The boundaries of a racial group are given not by biology (although recent attempts to apply cladistics to the concept of race try to show otherwise) but by social conventions that have a cultural and political history and geography (Gannett, 2004).

In addition to the difficulty of coherently and consistently defining race in biological terms, there is evidence that racial, ethnic, and other categories have limited capacity to predict the sort of bodily or physiological differences important to explain individual behavior and psychopathology. Visible or invisible phenotypic or genetic differences may or may not have any correlates with physiological systems that have behavioral consequences. For example, being blond or blue-eyed may be associated with an increased tendency for behavioral inhibition and shyness and hence greater risk for developing social phobia or anxiety (Moehler et al., 2006; Rosenberg and Kagan, 1989). Thus, there may be specific circumstances in which observable traits or characteristics that are associated with ethnoracial categories provide clues to vulnerability to a particular form of psychopathology. But the tendency to generalize from the correlates of phenotypic traits to racial or ethnic categories goes far beyond what might be empirically and statistically justified.

The search for correlates between membership in an ethnoracial group and psychological or psychopathological characteristics is problematic for many reasons: (i) it tends to ignore variation within the group; (ii) it may misinterpret context-dependent states as intrinsic traits; (iii) it overstates the generalizability or real-life significance of the correlations found in controlled experimental circumstances terms for behavioral outcomes in real-life situations; (iv) it ignores other mediating or moderating social factors that interact with the identified trait or state to give rise to the behavioral outcomes of interest; and (v) most fundamentally, it contributes to reifying socially constructed categories that may themselves be causes of discrimination and disadvantage. While it might be argued that these limitations are not relevant to an experimental program aimed at isolating specific causal mechanisms, research that ignores the socially constructed nature of racial and ethnic groups runs the risk of mistaking correlations with ethnicity that are contingent on social context for evidence of intrinsic characteristics.

Of course, to say that categories are socially constructed does not mean they have no impact on our lives. There are many ways in which social construals of race and ethnic identity can feed back into individuals' experience of self and the ways that others treat them (Wade, 2004) and these experiences may, in turn, have profound effects on psychopathology. Tracing the genealogy of constructs of race, ethnicity, or religious identity does not make these categories any less potent. The vocabulary of race and racism remains important not only because it is the most succinct way to refer to an area of social problems but also because social context configures experience in such a way that the separate processes that might be teased apart by observational or experiment studies — for example, the impact of discrimination and "microaggression" on blood pressure, or of poverty on maternal child-rearing strategies — are not truly separate events in the real world but come to us already configured and interacting in ways that reflect systemic patterns of social adversity or structural violence. Hence, the interest of medical anthropologists in the concept of "social suffering" (Kleinman et al., 1997) as a supplement to the medical focus on individual suffering — not because social suffering names any discrete entity or even a specific type of situation, but precisely because it draws attention to the social level of organization, in which a variety of material, interpersonal, and environmental circumstances may routinely co-occur and complicate or compound each others' effects over time.

Culture and psychopathology

In parallel with the changing concepts of culture, cultural psychiatry has reframed notions of the role of culture in psychopathology. Early forays in cultural psychiatry were much concerned with the phenomena that appeared unique to specific cultural groups, resulting in lists of "culture-bound" syndromes (CBS). DSM-IV incorporated about 25 of these into Appendix I, which was originally intended to serve simply as a glossary of terms that appear elsewhere in the text but which has had the inadvertent effect of reifying these syndromes. This is especially unfortunate because, with hindsight, many of the CBS listed are neither syndromes nor culture-bound. Most of the classic CBS are better understood as either folk illness labels and explanations (like "*susto*," a term applied in many Central or South American cultures to illnesses or afflictions attributed to a fright) or as *cultural idioms of distress* (like "*nervios*," a commonly used expression to refer to nonspecific stress and distress). Then too, many of these symptoms, syndromes, idioms, or explanations are not strictly bound to one culture but found in cognate forms in many different cultures and social settings, not just because of cultural diffusion but because the syndrome results from similar conceptual models, social practices, or embodied experiences (Kirmayer, 2007a; Kirmayer and Bhugra, 2009).

Consistent with the emphasis on CBS, early work in cultural psychiatry made a distinction between *pathogenic* factors (that may cause or contribute to psychopathology) and *pathoplastic* factors (that shape the expression or course of a psychopathological process). Behind this distinction is the assumption that forms of psychopathology can be classified according to underlying causes and mechanisms and that the subsequent symptomatic expression and ways of coping are incidental to this basic core. This scheme oversimplifies the potential relationships between social or cultural factors and psychopathology.

Table 1, drawing from Fiske (2009), summarizes some of the many ways in which culture may influence psychopathology, which may occur across the lifespan from earliest development, through the biological and social changes associated with important life transitions, to the adaptations of old age. The trajectories of psychopathology may involve long arcs of causation in which hereditary and early development create certain vulnerabilities, while later exposure to stressful circumstances associated with social status, migration, or cultural change contributes to overtaxing the individual's capacity for

Table 1. Cultural influences on psychopathology and healing

Biocultural systems	Cultural variations in system	Effects on psychopathology	Modes of coping, adaptation, and healing
Attachment	Development of secure base	Difficulties with attachment and separation	Relationship and social supports
Attention	Development of attentional systems (Posner and Rothbart, 2007); regulation of modes of attention by cognitive strategies, social cues, and contexts	Disorders of attention; dissociative disorders (Seligman and Kirmayer, 2008); symptoms and behaviors exacerbation by attention: anxiety, tension-related somatic symptoms, movement disorders (Tourette's) (Raz et al., 2007)	Meditation (Tang et al., 2007); trance and hypnosis (Raz, 2008); placebo effects (Raz, 2008)
Perceptual processing	Context dependence/ independence (Nisbett and Miyamoto, 2005)	Disorders of perceptual processing	Perceptual training
Attributions of causality	Dispositional biases related to concepts of personhood (Nisbett, 2003)	Attributional problems; vulnerability to depression and anxiety; somatized clinical presentations	Reattribution therapy
Emotion regulation	Styles of emotional expression	Psychophysiological consequences of emotion suppression or amplification	Expressive and cathartic therapies
Language	Differences in first and second language acquisition	Association of language and idioms with memory and emotion	Evocative use of metaphoric language; suggestive effects of images and instructions
Self-representations	Cultural concepts of personhood (Zhu et al., 2007)	Types of insult and injury to self; modes of narrating distress	Insight and narration (Kirmayer, 2007c)
Social interaction	Sources of interpersonal stress and social support; empathy	Difficulties in interpersonal interaction (relational disorders) (Beach, 2006); conflict with familiar (in-group) and unfamiliar (out-group); impact of racism and discrimination (through microaggression, rejection, and social marginalization) (Eisenberger et al., 2003; Krill and Platek, 2009; Richeson and Shelton, 2003)	Interpersonal support
Symbolic interaction	Classical conditioning; laws of sympathetic magic	Conditioned emotional responses (PTSD, phobias)	Healing amulets, talismans, and ritual actions (Kirmayer, 2007a)

adaptation, leading to illness. Indeed, since it appears that most types of psychopathology do not involve a single causal factor or event, but rather an interaction between multiple factors over time resulting in vicious cycles of symptom exacerbation, the distinctions between cause symptomatology, and course may be difficult to make (Kirmayer and Bhugra, 2009).

Further, to the extent that cultural modes of interpreting and coping with symptoms may contribute directly to pathology, the distinction between pathogenesis and pathoplasticity breaks down. A clear example is provided by the work of Hinton et al. (2007) identifying culture-specific modes of panic disorder among Southeast Asian refugees seen at a mental health clinic in the United States. Some of these patients suffer from panic attacks created by catastrophic thinking triggered by sensations of dizziness from orthostatic hypotension, twisting the neck, or a perceived change in body temperature. While the vicious circle of bodily sensation, cognition and emotion characteristic of panic disorder can be recognized in all of these cases, the loop depends on specific cultural interpretations of sensations; without these culture-specific attributions, there would be no vicious circle and no panic attack. So the cultural explanation and attribution are an essential part of the causal mechanism (Kirmayer and Blake, 2009).

There is evidence that culturally mediated social factors may contribute to the onset, course, and outcome of major psychiatric disorders. As one of the most severe forms of psychopathology, schizophrenia tends to be viewed as a biological disorder. Indeed, after a period of interest in the importance of social factors in the causes, course, and outcome of schizophrenia, there has been a decline of research on social factors in schizophrenia in North America (Jarvis, 2007, 2008). This de-emphasis of social determinants has gone hand in hand with a search for genetic causes. However, the same studies that show significant heritability of psychotic disorders also demonstrate the importance of environmental factors, most of which are shaped or determined by culture (Kendler, 2008). At the same time, other lines of research provide more direct evidence for profound social effects in the causes and course of schizophrenia. There is substantial evidence, for example, that "black" (Afro-Caribbean and others) immigrants to the United Kingdom and other countries experience elevated rates of schizophrenia and this effect persists or even worsens in the second generation (Cantor-Graae, 2007; Cantor-Graae and Selton, 2005; Coid et al., 2008). Social factors related to racial discrimination remain the most likely explanation for this increased prevalence (Morgan et al., 2008).

Recent work suggesting that schizophrenia might be associated with the epigenetic modulation of multiple systems, while emphasizing another site where biological "accidents" can result in pathology (Mill et al., 2008; Petronis, 2004), also provides justification for looking more closely at exposure to social adversity as a potential determinant of the causes and course of psychosis (Robert, 2000). This research points to a more refined way of thinking about the interactions between the brain and the social environment — interactions that are strongly determined by cultural processes. Epigenetics breaks down the distinction between nature and nurture by showing the ways in which developmental experiences change the regulatory genome. Culture then can exert lasting influences at any stage of development by changes in gene regulation and neural processing, as well as through family interaction and social circumstances across the lifespan.

Culture and developmental psychopathology: the example of conduct disorder (CD) and aggression in adolescence

Some of the most powerful of effects of culture may be exerted through variations in child rearing that shape development. The prolonged plasticity of the brain from infancy through adolescence and young adulthood is precisely what allows the person to acquire and embody cultural knowledge (Wexler, 2006). Developmental cultural neuroscience is still at an early stage (Pfeifer et al., 2009; Ray, 2009) and understanding the interactions between cultural factors and specific trajectories in cognitive development is particularly challenging. In this section, we use the example of adolescent aggression, a feature of CD, which is the most commonly diagnosed childhood psychiatric disorder (Scott, 2007; Wakefield et al., 2002), to examine some of the conceptual challenges involved in bringing the current logic of cultural neuroscience to the study of psychiatric disorders. In particular, given that the prevalence of CD differs across environments, we suggest that cultural neuroscience should explore cultural explanations of aggression, as well as cultural critiques of the diagnostic classifications and practices that deem it to be deviant.

The study of the adolescent brain is currently a burgeoning field in cognitive neuroscience. MRI studies have demonstrated that anatomical maturation of the brain is much more pronounced and prolonged than previously thought, particularly in parts of the brain that have been associated with executive functions and social cognition such as prefrontal, parietal, and superior temporal cortex (Blakemore and Choudhury, 2006; Gogtay et al., 2006; Paus, 2005). The adolescent brain has also been of increased interest to researchers looking to neuroscience to shed light on biological explanations for the onset of psychiatric disorders at this stage of the lifespan (Cody and Hynd, 1999; Nelson et al., 2005; Pine and Freedman, 2009; Steinberg, 2008). There is increasing interest in the possibility that the maturational processes of the brain themselves may be of causal significance for certain forms of psychopathology. For example, Paus and colleagues suggest that developmental events during the maturation of frontotemporal pathways may help account for the onset during adolescence of many cases of schizophrenia (Paus et al., 2008).

Perhaps owing to increased attention to youth aggression, violence, and risk at the level of public health policy in the United States of America and United Kingdom (Viding and Frith, 2006; Soriano et al., 2004,), biological approaches to the study of aggression have recently multiplied. Among these efforts, neuroscientists are using structural and functional MRI to explore the role of atypical neurodevelopment in antisocial behavior, in particular, aggression, seen in adolescence (Boes et al., 2008; Decety et al., 2009; Herpertz et al., 2008; Paus, 2005; Stadler et al., 2007; Sterzer et al., 2007). Aggression is one of the primary diagnostic features of CD, the most commonly diagnosed psychiatric disorder among children, with a prevalence reported to be around 5% in urban populations in the United States of America and the United Kingdom (Kazdin, 1995; Rutter et al., 1975). Along with the renewed interest in biological approaches, social and cultural factors are recognized as key issues for understanding and intervening in youth aggression.

How can cultural neuroscience investigate the role of culture in aggression and CD, without reducing aggression simply to a vulnerability detectable in the individual brain, that may be found more frequently in certain groups? From the start, brain and culture must not be considered as separate during ontogenic development. The concepts of bio-cultural co-constructivism capture this essential insight by insisting that the brain and culture are mutually dependent systems; both are in continuous and reciprocal interaction, simultaneously shaping and constraining each other and co-constructing developmental outcomes and potentials. This co-production is made possible through the prolonged (though limited) endogenous and exogenous plasticity at the levels of genes, neurons and their networks, cognition, and behavior, as well as social and cultural contexts (Baltes et al., 2006). Understanding the mechanisms of interaction across these levels is crucial if cultural neuroscience is to advance our understanding of developmental psychopathology.

Mapping aggression in the adolescent brain: neurobiology of conduct disorder

Aggression, defined clinically as disruptive and destructive behavior that causes harm to other people or animals, can take many forms, have many meanings, and occur for multiple reasons. Several lines of research have explored the biological basis of aggression, and have suggested that aggressive behavior is associated with individual differences in neuroendocrine and neurotransmitter system (Pihl and Benkelfat, 2005; Van Goozen, 2005) as well as inheritance of callous-unemotional traits (Viding et al., 2007), differences in cortisol levels in response to stress (Fairchild et al., 2008), and cognitive differences in impulse control and attention (Séguin and Zelazo, 2005; White et al., 1993). Recent neuroimaging studies have investigated the role of the brain in mediating these individual differences. Studies indicate differences between aggressive adolescents and controls, in terms of the functional activation of amygdala, striatum, and prefrontal cortex (Decety et al., 2009; Herpertz et al., 2008), volumetric structure in anterior cingulate (Boes et al., 2008), insula and amygdala (Sterzer et al., 2007), and structural and functional connectivity of frontal and temporal brain areas (Decety et al., 2009; Paus, 2005).

Although studies differ in their precise findings, neuroimaging results suggest a disruption in the circuitry of emotion regulation in aggressive adolescents. For example, in a recent fMRI study, Decety et al. (2009) found that when diagnosed aggressive adolescents observed others in pain, they activated neural systems linked to empathy, recruited the reward system to a greater extent, and displayed hypoactivity in amygdala, which suggested diminished ability to regulate their resulting emotion. Despite the interest of this work, there are many links in the conceptual chain from identifying putative neural correlates of aggressivity to the tasks of understanding, diagnosing, and intervening in adolescent CD.

The role of culture in conduct disorder

Most studies investigating the neurobiological manifestations of aggression in adolescents with CD, including the work cited above, have been done in Europe and North America using European or Euro-American participants. Examining a psychiatric disorder across cultures, however, demands a valid and reliable measure of the disorder than can be applied to different populations living in disparate contexts. Recent cross-cultural and cross-national studies reveal large variations in reported prevalence both within and between countries, as well as a dramatic increase in reporting of externalizing behaviors in the United States of America in recent years, and very high rates of comorbidity of CD with other "disruptive" disorders such as attention deficit hyperactivity disorder (ADHD) (Chen et al., 1998; Lewis et al., 1984; Wakefield et al., 2002; Richters and Cicchetti, 1993). For example, prevalence rates of CD have been reported to differ between adolescents of different immigrant communities in the host countries of Canada and in the United States of America (Bird, 1996; Chen et al., 1998; Rousseau et al., 2008; Shaffer and Steiner, 2006; Smokowski and Bacallao, 2006).

Like most psychiatric disorders, there are no biomarkers for CD and the diagnosis cannot be made or verified with a laboratory test. In the absence of such a test, cultural differences in rates of diagnosis and the diverse social contexts of misconduct pose challenges for brain research on CD. Interpreting cross-cultural differences is complex, and if the identification of cognitive or neural correlates is to play a role in understanding CD, then cultural neuroscience must pay close attention to the sociocultural context of the individual and of the diagnostic process itself.

Some critics have argued that the current approach to the diagnosis of CD which, like that of most psychiatric disorders, focuses on manifest behaviors such as aggression and lacks clear exclusion criteria, obscures other treatable symptoms and syndromes; this critique has raised doubts about the validity and usefulness of the CD diagnosis in any setting (Lewis et al., 1984; Richters and Cicchetti, 1993; Quay, 1987). Isolating aggressive behavior as a feature of CD provides a useful way to approach the question of cultural differences at the level of the brain using cognitive or neuroimaging methods. Given the challenges to cross-cultural validity of diagnostic categories as well as the heterogeneity and multifactorial origins of psychiatric disorders, it may be useful to adopt a symptom-based approach to design studies that unpack the diagnosis and examine the cultural contingencies of particular neurophysiological, neuroanatomical, cognitive, or neuropsychological dimensions (Helzer et al., 2008). This dimensional approach is useful for understanding how environmental contexts interact with gene-brain-cognition-behavior pathways in the development of childhood disorders (Knapp and Mastergeorge, 2009; Viding and Frith, 2006). While specific behaviors, biological markers, or endophenotypes (Gottesman and Gould, 2003) can be helpful in defining homogeneous groups within the symptom criteria, there are particular challenges to this approach in developmental psychopathology and cognitive neuroscience. The anatomical and functional changes in the brain during development, as well as the changing nature of psychopathologies, mean that it is difficult to interpret endophenotypes across development, for example, to identify the neurocognitive reflections of aggression at different age points (Viding and Blakemore, 2007).

At the same time, several researchers have developed a cultural critique of current psychiatric classifications that diagnose particular forms of conduct among children and adolescents as pathologically "antisocial." It has been suggested, for example, that CD is a product of Western cultures, which serves social and cultural purposes by biologizing socially undesirable behavior through medical research and managing the risk of such behavior through medical control (Conrad, 2005; Timimi, 2002). Critics of the CD diagnostic category emphasize the need for a cultural perspective on constructions of childhood, deviant behavior, and child-rearing practices to avoid shifting the focus of explanations and interventions from social context to individual biology exclusively.

The meanings and contexts of aggressive behavior

Both epigenetic and cultural approaches point to the need for a closer examination of the lived experience and cultural worlds of adolescents — that is, the particularities of the local environments (including family dynamics, expected roles, peer groups, socioeconomic status, experiences of racism, and discrimination) that are the context of aggression — to better understand aggressive "disorders." Cross-cultural research on CD highlights the importance of investigating the similarities and differences across cultures in values of independence, interdependence, compliance, or aggression in childhood and adolescence, as well as the specific social contexts of misconduct (Chen et al., 1998; Shaffer and Steiner, 2006; Smokowski and Bacallao, 2006). The determination that aggression or other behavior is socially transgressive or psychopathological depends on the economic, political, and cultural systems in which it occurs and throug which it is interpreted as a problem for clinical attention.

Ethnographic research has shown that in some small-scale societies, adolescent boys are exposed to aggressiveness around puberty and their own expressions of aggression can be socially approved (Herdt and Leavitt, 1998; Rosaldo, 1980). In other societies, adolescent aggression among boys seems to be rare (Broch, 1990). It has been suggested that higher levels of aggression are seen in industrial contexts in which there is greater socioeconomic complexity and inequality associated with the competitiveness and economic disparities of capitalist development (Fabrega and Miller, 1995). However, aggression can play an important role in adolescents' ecological adaptation in such settings and may be highly socialized (Sharff, 1998). In these industrialized, urban settings, certain disadvantaged groups seem to be at higher risk of a CD diagnosis. Given the various meanings of aggression, a question for cultural neuroscience, then, is whether socially sanctioned and socially prohibited forms of aggression are mediated by differential neurocognitive mechanisms. Differences in aggressive behavior in different contexts may reflect cultural modulation of affect both during early development and through cognitive strategies used by adolescents to amplify or reduce anger or other specific emotions (Hollan, 1988; Hollan and Wellenkamp, 1994).

Our discussion to this point has considered culture in terms of the lived experience and ways of life of adolescents, which may include aspects of social institutions, as well as individuals' knowledge, attitudes, and practices. However, as mentioned earlier, socially constructed categories of ethnic or group identity may also be important and relate to aggression. In the United States, for example, the epidemiology of youth violence finds that "African-Americans and Latinos are overrepresented among both offenders and victims of violence" (Soriano et al., 2004). This research on adolescents belonging to minority ethnic communities demonstrates that the development of aggressive behaviors cannot be viewed as simply individual psychological dysfunction but rather must be seen as a response to a number of specific environmental stressors. For example, using their case study of Latino adolescents in the United States of America, Shaffer and Steiner (2006) emphasize the importance of addressing the cultural identity of the individual, going beyond the category of "Hispanic" to consider the degree of acculturation or acculturative stress, and examining the relationship between the stress involved in acculturation and the behavioral criteria of CD. They stress that a comprehensive approach to understanding aggression and CD in adolescents requires the development of conceptual and methodological tools to study the complex interplay between ethnicity, the experience of migration, urbanization, acculturation, family dynamics, socioeconomic status and inequality, racism, and government policy.

Stressors such as racism, intergenerational, and parental conflict can adversely affect identity formation, a primary aspect of normal adolescent development.

Drawing normative conclusions about cross-cultural differences based on differences in functional activity in the brains of groups of adolescents from different ethnic backgrounds therefore may be conceptually misleading and methodologically flawed, and by diverting attention from historical and social contextual issues, it may have important social and political consequences (Connors and Singh, 2009; Johnson et al., 2002). Rather than studying the impact of culture on the brain in aggression by categorizing groups on the basis of ethnic identity, cultural neuroscience might use more meaningful distinction such as measures of perceived racism, quality of relationships with parents, or particular beliefs or attitudes could be correlated with performance on emotion processing tasks and measures of aggression to investigate the neurocognitive mechanisms that mediate associations between particular stressors and aggression. A similar approach has been taken in developmental cognitive neuroscience to investigate the relationship between socioeconomic status in the United States and executive function abilities and disparities (Hackman and Farah, 2009).

Coming of age in a globalizing world

Historical constructions of the nature of normal adolescence, cultural meanings of aggression, the ongoing medicalization of youth deviance and aggression, and the technologies of psychiatric epidemiology and diagnosis all play a role in current approaches to CD and the explanatory role of the brain in adolescent behavioral development (Choudhury, in press; McKinney, 2008). Larger societal changes have constructed adolescence as a time of turmoil and obscured the ways in which society itself has diminished the opportunities to take on meaningful roles and responsibilities that might channel youthful energy and aggression in socially constructive ways. The normal aggression of youth is met with aggressive marketing as part of the machinery of consumer capitalism. When successful, this creates docile consumers; when matched by economic disparities and injustices, it produces angry and disaffected youth suffering from a sense of anomie. Beyond this general problem of the appropriate expression of the expanding energies and possibilities of youth, there are a host of specific geopolitical problems related to migration, urbanization, and globalization that serve to accentuate inequalities and aggravate social pathology and attendant psychopathology. Psychiatric diagnostic constructs and interpretations of behavior have global currency and are increasingly exported and introduced into diverse social and cultural settings. Globalization has also transformed the life-worlds of adolescents in many societies, introducing new technologies of communication and corresponding forms of identity and community. Far from being distractions from the development of a cultural neuroscience of psychopathology, we believe neuroscientists must engage with these sociopolitical changes to formulate relevant research questions and meaningfully interpret their results.

Conclusion

We have tried to show how the application of cultural neuroscience to psychopathology depends crucially on how we understand culture. Culture is not just a matter of cognitive content or processes, and it cannot be captured through an epidemiology of representations. Cultural systems reside both in the individual and in the social institutions, routines, and practices — both local and global — in which each individual participates. These systems give rise to ethnic and cultural identities but also to ways of life that cut across recognized ethnocultural categories. Despite the promise of cultural neuroscience for psychiatry, there are reasons to be concerned about locating culture in the brain because this may serve to reify these identities and obscure their social origins.

We have used the case of adolescent aggression, a feature of CD, to examine some of the conceptual challenges involved in developing a cultural neuroscience that can inform psychiatric explanations and interventions. We suggest that cultural neuroscience must grapple not only with the cultural factors involved in the onset, course, and outcome of disorders and their unequal distribution in the population but also with the cultural and historical embedding of psychiatric nosology itself. If cultural neuroscience is to contribute to mental health theory and practice, experimental designs require careful conceptualization of both culture and psychopathology. Rather than uncritically accepting the received categories as applicable across cultures, a more effective methodological strategy to demonstrate the impact of culture on psychopathology would begin by decomposing discrete diagnostic categories into functional systems, dimensions, and underlying processes. Similarly, constructing meaningful "cultural groups" for comparison depends on identifying the dimensions of culture relevant to a specific form of psychopathology. These dimensions can be measured independently of individuals' cultural identities or affiliations. This will allow the researcher to identify correlations between cultural dimensions, psychopathological processes, and behavioral outcomes, which is also useful for designing interventions and evaluating their efficacy. For example, the systems underlying aggressive behavior are likely to be tuned through social or environmental interactions over the course of development. Future research may shed light on how interventions including educational approaches, remedial parenting, rites of initiation, social mentoring programs, involvement in certain cultural practices, or other forms of cultural identification and engagement can influence developmental pathways to reduce the likelihood of aggressive behavior or conduct disorder (Blakemore and Frith, 2007; Smokowski and Bacallao, 2006).

Beyond the strategy of unpacking culture and psychopathology into their underlying dimensions relevant to specific functional systems and behavioral outcomes, there is a need for a critical perspective on the received categories used to diagnose psychopathology and assign individuals to specific cultural groups. Clinical assessment must be mindful of the ways in which psychopathology, symptom experience, and diagnostic systems are shaped by social and cultural contexts and embedded in cultural systems of meaning. Scientific inquiry also requires critical reflection about the origins of the categories we use.

Recently, there has been much emphasis in neuroscience and genetics on the interactions between the brain and environment. Research on epigenetics has begun to reveal how interactions of the genome with the environment over the course of development lead to structural changes in the methylation patterns of DNA that regulate cellular function. These changes may be lasting, so that experience remodels the functional genome. There is compelling evidence, for example, that early parenting experiences alter the regulation of stress response systems for the life of the organism (Fish et al., 2004; Meaney and Szyf, 2005; Weaver et al., 2004). This work challenges the facile divide of nature and nurture. If cultural neuroscience is to advance, it must develop new conceptual models that capture the interactions of brain and environment central to developmental and social processes. The tenacious divide between nature and nurture has served to maintain a division of labour between the disciplines and widened the gulf between those who study the brain and those concerned with the (physical, social, political) environment "outside" the person.

Biology itself, however, demonstrates that brain and environment form an interacting system. Cultural factors structure the distribution of genes in a population, their modulation over the course of neurodevelopment, and the functioning of the brain in social contexts across the lifespan. The same studies that demonstrate the role of genetic and constitutional factors in psychopathology also show the wide influence of social and environmental factors, pointing toward the importance of culture in understanding psychopathology. The advances of cultural neuroscience will allow us to sharpen our questions about the impact of culture on the causes, course, and outcome of psychiatric disorders.

Cultural influences on psychopathology are not only inscribed in the brain over the course of development, but also reside in social practices that create situations that are challenging for specific groups or individuals. A hierarchical systems view would argue that certain interactional and meaning-centered aspects of culture that reside in social institutions and practices can never be fully captured by neuroscience (Henningsen and Kirmayer, 2000). There will always remain a need for other conceptual vocabularies, constructs, and methodologies to understand these emergent levels of organization (Kirmayer et al., 2007). Cultural neuroscience can be most fruitfully developed through ongoing dialogue with the social sciences that illuminate these fundamental constituent levels of human experience.

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SECTION VII

Conclusion

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CHAPTER 20

Cultural neuroscience: a once and future discipline

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Abstract: The study of culture and biology has long stood stratified within the social and natural sciences, a gap that physicist C.P. Snow (1959) famously called "the two cultures." Cultural neuroscience is an emerging, interdisciplinary field that examines the bidirectional influence of culture and genes to brain and behavior across multiple timescales. Integrating theory and methods from cultural psychology, brain sciences, and population genetics, cultural neuroscience is the study of how cultural values, practices and beliefs shape brain function and how the human brain gives rise to cultural capacities and their transmission across macro- (e.g., phylogeny, lifespan) and micro timescales (e.g., situation). The current article presents the aims and methods of cultural neuroscience, highlights recent empirical findings in the field, and discusses the potential implications of this field for bridging the social and natural sciences as well as informing interethnic ideology and population health concerns, more broadly construed.

Keywords: cultural neuroscience; culture; brain; fMRI; ERP; culture–gene coevolution; transcultural neuroimaging

Introduction

> Why are the tribes and nations of the world different, and how have the present differences developed? — Franz Boas (1907)

The nature and origin of human cultural diversity has been a rich source of intellectual curiosity for scholars since the first millennium. Early in the 7th century, Isidore of Seville observed in one of the earliest written encyclopedias, *Etymologiae*, that humans vary both in physical appearance and ways of thinking (Jahoda, 2002). Centuries later, philosophers, such as Descartes and Locke, renewed debate on the origin of human diversity in thinking and behavior. During the Age of Enlightenment, the study of human diversity accelerated with the emergence of two enormously influential, but divergent, schools of thought: evolutionary biology and modern anthropology. Darwin's theory of evolution led to the development of the field of evolutionary biology, which explained diversity in the biological world as emerging from the universal process of natural selection. By contrast, pioneering anthropologists, such as Franz Boas and Margaret Mead, favored scientific approaches to culture that emphasized relativism whereby human cultures were best understood on their own terms, rather than as products of transparent universal laws, including those of a biological nature (Lewis, 2001).

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Following Darwin and Boas, the scientific study of biology and culture largely continued to diverge, even with the emergence of nexus fields, such as psychology, which would appear well-positioned to formally integrate theory and methods across the social and natural sciences. Evolutionary psychologists, for instance, argue that the human mind and behavior are best understood as adaptations or functional products of natural selection and embrace neuroscience as a means uncovering universal neural circuitry specialized for solving different adaptive problems (Barkow et al., 1992). Widely adopted by modern cognitive neuroscientists, this evolutionary approach to the study of the human brain has proved enormously fruitful for generating sound hypotheses and evidence for how discrete brain structures map onto distinct kinds of adaptive psychological functions (Caramazza and Shelton, 1998; Dehaene and Cohen, 2007; Kanwisher et al., 1997). However, this evolutionary emphasis has also steered much scientific attention within cognitive neuroscience toward the study of universal, rather than culturally specified, neural mechanisms and behavior. By contrast, cultural psychologists have largely focused on investigating the mutual constitution of culture and the human mind and have convincingly constructed theories and discovered evidence that culture shapes nearly every facet of psychology and behavior (Kitayama and Cohen, 2007). However, as a consequence, cultural psychologists have spent less time thinking about how to meaningfully integrate theories of human culture with theories of human evolution and how cultural values, practices, and beliefs shape not only mental, but also neurobiological, processes.

The past century has witnessed a number of theoretical attempts within psychology to integrate cultural and neurobiological approaches in the study of the human mind and behavior. For instance, prominent developmental psychologists, such as D'Arcy Thompson and C. Waddington, introduced early notions of probabilistic epigenesis, whereby humans come into the world with sets of possible developmental trajectories that are then pursued or not over the course of the lifespan as a result of interactions with the cultural environment (Johnson, 1997). More recently, biocultural co-constructivism theory has emerged as a way of explaining how developmental trajectories unfold via interactions between genetic and cultural factors, and importantly, how neural plasticity may later both developmental trajectories and the end state (Li, 2003).

Despite rich theoretical motivation for studying culture–biology interactions within the human brain, precise empirical demonstrations and theoretical models of bidirectional relationship between cultural and biological mechanisms (e.g., culture–gene; culture–brain; culture–brain–gene) have largely remained elusive. A number of factors have contributed to the current knowledge gap. First, empirical studies of neural substrates underlying human emotion and cognition have typically been informed first by empirical evidence in non-human animals (Davidson and Sutton, 1995; Gazzaniga et al., 2002). However, since cultural competence is predominantly a human achievement (Dehaene and Cohen, 2007; see also, Tomasello et al., 2005) it is not possible for behavioral neuroscience models of culture to inform human neuroscience investigations of culture. Second, until recently, researchers have lacked technology to study these questions in humans. For instance, the field of human neuroimaging began to flourish only within the past two decades (Fig. 1a). Third, there is typically a lack of awareness among researchers about the growing research bias in the populations that they study (Arnett, 2008). Within the field of psychology, 95% of psychological samples come from countries with only 12% of the world's population (Arnett, 2008). Within the field of human neuroimaging alone, 90% of peer-reviewed neuroimaging studies come from Western countries (Fig. 1b). Moreover, a growing number of critical neuroscientists are beginning to document how such researcher biases affect how neuroscientists construct theories and design future experiments (Choudhury et al., 2009). Hence, our current state of knowledge of mind–brain mappings is largely restricted to scientific observations made of people living within Western industrialized nations, leaving a large empirical gap in our

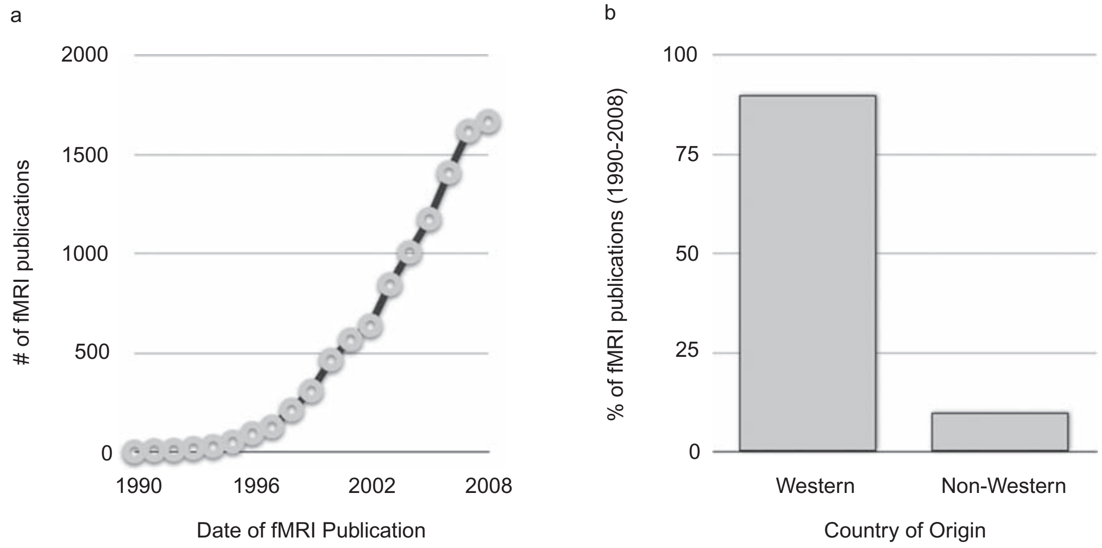

Fig. 1. Growth trends and publication bias in peer-reviewed human neuroimaging literature. (a) Graph illustrating the growth in peer-reviewed human neuroimaging studies from 1990 to 2008; (b) graph illustrating the publication bias within the human neuroimaging literature whereby the vast majority (~90%) of publications to date originate from a Western country.

understanding of how diverse cultural environments affect the human mind, brain, and behavior.

What is cultural neuroscience?

Cultural neuroscience is an emerging research discipline that investigates cultural variation in psychological, neural, and genomic processes as a means of articulating the bidirectional relationship of these processes and their emergent properties (Fig. 2). Research in cultural neuroscience is motivated by two intriguing questions of human nature: how do cultural traits (e.g., values, beliefs, practices) shape neurobiology (e.g., genetic and neural processes) and behavior and how do neurobiological mechanisms (e.g., genetic and neural processes) facilitate the emergence and transmission of cultural traits?

The idea that complex behavior results from the dynamic interaction of genes and cultural environment is not new (Johnson, 1997; Li, 2003; Caspi and Moffitt, 2006); however, cultural neuroscience represents a novel empirical approach to demonstrating bidirectional interactions between culture and biology by integrating theory and methods from cultural psychology (Kitayama and Cohen, 2007), neuroscience (Gazzaniga et al., 2002), and neurogenetics (Canli and Lesch, 2007; Green et al., 2008; Hariri et al., 2006). Similar to other interdisciplinary fields such as social neuroscience (Cacioppo et al., 2000) or social cognitive neuroscience (Ochsner and Lieberman, 2001), affective neuroscience (Davidson and Sutton, 1995), and neuroeconomics (Glimcher et al., 2008), cultural neuroscience aims to explain a given mental phenomenon in terms of a synergistic product of mental, neural, and genetic events. Cultural neuroscience shares overlapping research goals with social neuroscience, in particular, as understanding how neurobiological mechanisms facilitate cultural transmission involves investigating primary social processes that enable humans to learn from one another, such as imitative learning. However, cultural neuroscience is also unique from related disciplines in that it focuses explicitly on ways that mental and neural events vary as a function of culture traits (e.g., values, practices, and beliefs) in some meaningful way. Additionally, cultural neuroscience illustrates how cultural traits may alter neurobiological and psychological processes beyond those that facilitate social experience and behavior, such as perception and cognition.

Why study cultural influences on brain function?

There are at least three reasons why understanding cultural and genetic influences on brain function likely holds the key to articulating better psychological theory. First, a plethora of evidence from cultural psychology demonstrates that culture influences psychological processes and behavior (Kitayama and Cohen, 2007). To the extent that human behavior results from neural activity, cultural variation in behavior likely emerges from cultural variation in neural mechanisms underlying these behaviors. Second, cultural variation in neural mechanisms may exist even in the absence of cultural variation at the behavioral or genetic level. That is, people living in different cultural environments may develop distinct neural mechanisms that underlie the same observable behavior or recruit the same neural mechanism to varying extents during a given task. Third, population variation in the genome exists, albeit on a much smaller scale relative to individual variation, and 70% of genes express themselves in the brain (Hariri et al., 2006). This population variation in allelic frequency in functional polymorphisms, such as those that regulate neural activity, may exert influence on subsequent mental processes and behavior. To the extent that behavior arises from neural events and both cultural and genetic factors influence neural events, a comprehensive understanding of the nature of the human mind and behavior is impoverished without a theoretical and empirical approach that incorporates these multiple levels of analyses.

Theory and methods in cultural neuroscience

The current ability to discover cultural variation across multiple levels of analysis is now possible in ways never previously imagined, due in large part, to fortuitous theoretical and methodological advances in three distinct fields: cultural psychology, brain sciences, and neurogenetics (Figs. 2 and 3). In recent years, cultural psychology has made major advances in identifying cultural traits that characterize the diversity in social groups around the world as well as articulating the criteria for creating culturally appropriate behavioral measures that ensure the psychological phenomena of interest is testable in people of all cultures (Kitayama and Cohen, 2007; Norenzayan and Heine, 2005). Human neuroscience, including cognitive, social, and affective neuroscience, has revolutionized the study of the mind and brain by developing an arsenal of techniques for mapping neural

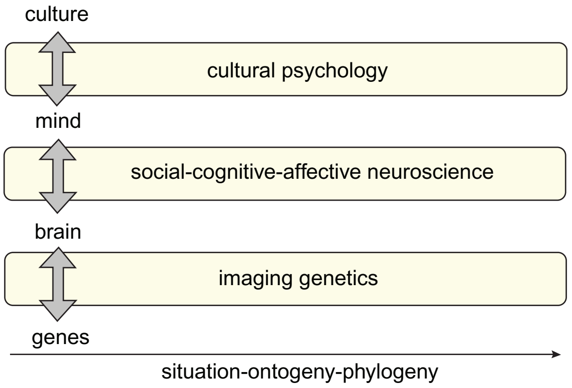

Fig. 2. Illustration of the cultural neuroscience framework, integrating theory from cultural psychology, social/cognitive/affective neuroscience, and neurogenetics.

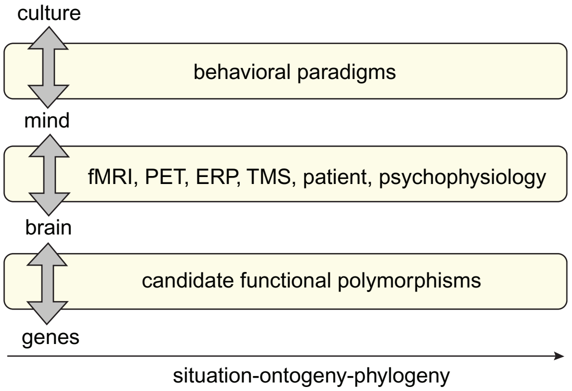

Fig. 3. Illustration of the cultural neuroscience toolbox, integrating methods from cultural psychology, social/cognitive/affective neuroscience, and population genotyping.

processes to psychological processes at varying degrees of spatial and temporal resolution (Gazzaniga et al., 2002; Handy, 2005; Heeger and Ress, 2002). Molecular biology has witnessed major transformations in the scope of data and techniques now available for understanding the structure and function of the human genome. From techniques for studying the association between single genes and behavior to genome-wide maps that assess the association of the entire genome to a given behavior, the development of molecular biology techniques has led to an explosion of possible ways for mapping genes to neural, mental, and cultural processes. Taken together, the convergence of these tools enables unprecedented ability to investigate the mutual constitution of genes, brain, mind, and culture.

Cultural psychology

Theory and methods of cultural psychology comprise the first component of the cultural neuroscience toolbox. First, cultural psychologists have developed rich set of theoretical constructs that specify what kinds of cultural values, practices, and beliefs reliably impact human behavior. For instance, Hofstede (2001) proposed that cultures could be distinguished according to five cultural dimensions: *individualism–collectivism*, *uncertainty avoidance*, *power distance*, *long-term/short-term orientation, and masculinity/femininity*. The cultural dimension of *individualism–collectivism*, in particular, has been shown to reliably affect a wide variety of human mental processes at a behavioral level, including self-concept, motivation, perception, emotion, and cognition (Markus and Kitayama, 1991; Triandis, 1995). Individualism refers to when individuals construe themselves as separate and autonomous from each other, whereas collectivism refers to when individuals construe themselves as highly interconnected and defined by their relations and social context. Another potent cultural construct is *holistic* versus *analytic cognition*, a dimension thought to characterize differences in thinking styles between Westerners and East Asians. East Asians are thought to primarily engage in holistic cognition, attending to the entire field of a scene and relying on dialectical reasoning, whereas Westerners have been shown to primarily exhibit analytic cognition, attending to objects more than their context and using rules, such as formal logic, to understand reason about themselves and the world (Nisbett et al., 2001). Finally, *socio-economic status or social class* has been shown to serve as an important cultural lens shaping one's sense of free will, choice, and related behaviors (Snibbe and Markus, 2005; Savani et al., 2008). These cultural dimensions provide a core theoretical foundation from which cultural neuroscientists can formulate novel hypotheses about how and why culture may influence brain functioning. Formulating sound hypotheses about how cultural traits modulates neural mechanisms a priori is critical to building better theories about how culture shapes neural systems and why as well as ensuring that evidence of cultural variation in neural systems is not misinterpreted as evidence for essentialist theories of race (Tate and Audette, 2001).

Second, cultural psychologists have developed a number of novel behavioral methods for investigating cultural influences on behavior. First, a popular and effective way of measuring cultural traits is via *behavioral surveys*. Indeed, a lion's share of prior cultural psychological research has been focused on creation and validation of cultural value surveys, such as those used to measure individualism and collectivism (Singelis, 1994). Importantly, cultural psychologists have discovered that people living in diverse cultural value systems demonstrate different types of response biases when completing behavioral surveys. For instance, collectivists tend to show moderacy biases, such that they respond to items using the midpoint of Likert scales, whereas individualists tend to show extremity biases, such that they typically respond to items using the endpoints of Likert scales (Heine, 2008). Understanding when and how these response biases may emerge is critical for cultural neuroscientists wishing to map cultural variation in behavior to cultural variation in neural functioning.

Another important cultural psychological method is *situational sampling*. One of the hardest challenges in designing cross-cultural experiments is in ensuring that one's experimental stimuli have the intended meaning across cultures. Situational sampling refers to a technique for generating experimental stimuli that are optimized to reveal cultural variation in behavior. In experiments utilizing situational sample, researchers ask participants from the two or more cultures of interest to generate example of the phenomena of interest. Then, these examples are used as stimuli in a subsequent experiment to test cultural variation in responses to the culturally specific stimuli (Heine, 2008).

A third cultural psychology technique important for conducting cultural neuroscience research is *cultural priming* (Hong et al., 2000; Oyserman and Lee, 2008). Often, cross-cultural psychologists conceptualize nation or race as a proxy for culture; however, such gross characterizations of culture are impoverished as they fail to capture the individual variability within cultures, the dynamic nature of culture, and the fact that an individual can possess awareness of and appreciation for than one cultural system simultaneously. To address these important issues, cultural psychologists have developed cultural priming techniques to directly manipulate cultural value systems within mono- and multicultural individuals and to show how cultural values dynamically shape behavior. Cultural priming involves temporarily heightening individuals' awareness of a given cultural value system through either explicit (e.g., writing an essay about individualism) or implicit means (e.g., search for synonyms of individualism in a word search). A number of different types of cultural priming techniques have been successfully used to elicit cultural variation in a range of behavioral processes. Notably, prior research has revealed that not all cultural priming techniques have equivalent influence across domains; that is, some cultural priming methods are more likely to trigger cultural variation in social relative to cognitive processes and vice versa (Oyserman and Lee, 2008). Hence, when adopting cultural priming to study the direct influence of cultural values on neural mechanisms, it is important to select a cultural priming technique that is task-appropriate.

Human neuroscience

Cognitive neuroscience theory and methods comprise the second component of the cultural neuroscience toolbox. Recent decades have brought an unprecedented array of tools for directly and indirectly measuring human brain activity and relating this brain activity to behavior. There are several neuroscience tools that psychologists can use to map neural structure to mental function such as the following: functional magnetic resonance imaging (fMRI), positron emission topography (PET), transcranial magnetic stimulation (TMS), magnetoencephalography (MEG), event-related potentials (ERP), and lesion studies. Each tool has its strengths and weaknesses, particularly when comparing each tool's spatial and temporal resolution (Cacioppo and Decety, 2009). Neuroimaging techniques, such as fMRI and PET, record indirect neural activity and have very good spatial resolution (mm^3), but poor temporal resolution (seconds), relative to electrophysiological techniques such as ERP and EEG. By contrast, ERP and EEG record neural activity directly below the scalp and thus have excellent temporal resolution (milliseconds), but lack high spatial resolution. Newer hybrid techniques, such as MEG, combine the advantages of both brain imaging and electrophysiological techniques and it is likely that as medical technology improves, so will our ability to accurately record neural activity while awake humans perform mental tasks.

In addition to taking into consideration the spatial and temporal resolution of human neuroscience techniques, it is equally important to consider what kinds of questions can be addressed with each technique, and what questions remain unaddressed given the limitations of current methodologies. TMS and lesion studies enable researchers to address which brain regions are necessary for a given mental function, while brain imaging and electrophysiology provide tools for associating a given neural structure or processes to a given mental function. To date, most cultural neuroscience research has utilized cross-cultural or transcultural neuroimaging to demonstrate cultural variation in the magnitude of neural response to a given stimuli (Chiao and Ambady, 2007; Han and Northoff, 2008; Park and Gutchess, 2006). However, future research may also include novel methodologies, such as cross-cultural TMS or lesion studies, that will be able to address novel questions such as whether or not a given brain region is necessary for a given mental function in one culture, but not another.

Neurogenetics

The theory and methods from neurogenetics comprise the third component of the cultural neuroscience toolbox. Genes are the fundamental physical and functional unit of heredity. Genes substantially influence every level of human biology, including regulating neurotransmission within the brain. Recent advances in neurogenetics have led to major advances in our understanding of how genes regulate brain mechanisms underlying cognitive (Green et al., 2008), emotional (Hariri et al., 2006), and social behavior (Canli and Lesch, 2007).

Cultural variation is evident in the human genome for a number of reasons, albeit on a much smaller scale relative to individual genetic variation. Cultural variation in allelic frequencies of a given gene may occur due to number of evolutionary processes, such as natural selection and genetic drift. Natural selection may lead to differential frequency of gene variants when certain genetic variants confer reproductive advantages over another. Genetic drift may also result in changes in allele frequencies within populations over time, but in a more random manner. For instance, founder effects, a type of genetic drift, can lead to a loss of genetic variation when a new population is established by a very small number of individuals from a larger population.

Due to their robust allelic variation across cultures, two genes are likely to play a key role in future cultural neuroscience research: the serotonin transporter polymorphism (*5-HTTLPR*) and dopamine D4 receptor (*DRD4*) exon III polymorphism. The 5-HTTLPR consists of a 44-base pair insertion or deletion, generating either a long (l) or a short (s) allele. Evidence from behavioral genetics indicates that the S allele of the serotonin transporter gene (*5-HTTLPR*) is associated with increased negative emotion, including heightened anxiety (Munafò et al., 2005; Sen et al., 2004), harm avoidance (Munafò et al., 2005), fear conditioning (Lonsdorf et al., 2009), attentional bias to negative information (Beevers et al., 2007), as well as increased risk for depression in the presence of environmental risk factors (Caspi et al., 2003; Taylor et al., 2006; Uher and McGuffin, 2008, see also Munafo et al., 2009). In particular, exposure to chronic life stress, such as interpersonal conflict, loss, or threat, is considered a well-known environmental risk factor for depression in S allele carriers of the 5-HTT (Caspi et al., 2003). The s allele of the *5-HTTLPR* is extremely prevalent in East Asian populations (e.g., 70–80% s carriers) relative to other nations (e.g., 50% or less s carriers) (Chiao and Blizinsky, 2009; Gelernter et al., 1997). The dopamine D4 receptor (*DRD4*) exon III polymorphism has been linked to novelty seeking and pathological gambling (Chen et al., 1999). Individuals with the 7-repeat allele have higher novelty seeking scores than those with other *DRD4* variants (Chen et al., 1999). The 7-repeat allele is extremely prevalent in South American Indian populations (e.g., 70–80% 7-repeat carriers), but extremely rare in East Asian populations (e.g., <1% 7-repeat carriers) (Chen et al., 1999).

Importantly, genes not only regulate brain mechanisms and behavior, but also influence and are influenced by cultural selection (Boyd and Richerson, 1985). According to culture–gene coevolutionary theory, cultural traits can possess evolutionary advantages. For instance, cultural traits, such as individualism and collectivism (Fincher et al., 2008), may serve adaptive functions and thus, culturally consistent phenotypes may become selected for over successive generations, leading to population variation in allelic frequencies for certain genes. Additionally, a central claim of culture–gene coevolutionary theory is that once cultural traits are adaptive, it is likely that genetic selection causes refinement of the cognitive and neural architecture responsible for the storage and transmission of those cultural capacities (Boyd and Richerson, 1985). Hence, these evolutionary processes of cultural and genetic selection likely result in cultural variation in psychological and neural processes, which serve as endophenotypes or intermediate phenotypes of the cultural and genetic traits.

A central goal for cultural neuroscience research is to understand how these dual forces of cultural and genetic selection shape brain function and behavior. The field of neurogenetics provides the empirical means by which cultural neuroscientists can investigate similarities and differences in how genes regulate human brain function across cultures. More specifically, neurogenetics research enables cultural neuroscientists to identify neural endophenotypes or brain regions that may be influenced by culture–gene coevolutionary forces. For example, recent imaging genetics research has shown that people who carry the s allele of the *5-HTTLPR* exhibit greater amygdala response to emotional stimuli (Hariri et al., 2002) which is likely due to increased amygdala resting activation (Canli et al., 2005) and decreased functional coupling between the amygdala and subgenual cingulate gyrus (Pezawas et al., 2005), relative to individuals carrying the L allele. Future research in cultural neuroscience may examine the effect of cultural and genetic selection on amygdala response and emotional behavior. More broadly, by converging theory and methods from neurogenetics and cultural psychology, cultural neuroscientists are equipped to generate and test novel hypotheses not only about how genes or culture independently influence brain function, but also how genes and culture interact and mutually shape brain function across the lifespan and across successive generations.

Cultural influences on brain function: progress in cultural neuroscience

Not only does the human brain support the transmission of cultural values, beliefs, and practices via neural mechanisms of imitation (Iacoboni, 2009; Reynolds-Losin et al., in press), culture also dynamically shapes brain function across multiple timescales (Ambady and Bharucha, in press; Chiao and Ambady, 2007; Chiao, in press; Han and Northoff, 2008; Park and Gutchess, 2006; Wexler, 2006). Given the rich existing literature on how the brain facilitates cultural transmission (Iacoboni, 2009; Reynolds-Losin et al., in press), this next section will highlight illustrative empirical advances of the latter, namely how cultural values, beliefs, and practices influence neural mechanisms supporting a range of psychological domains, from perception and memory to emotion and social cognition.

Visual perception

Cultural beliefs, such as self-construal style, have been shown to influence visual perception at a behavioral level, as demonstrated by the Frame-Line Test (FLT) (Kitayama et al., 2003). The FLT measures one's capacity to both incorporate and to ignore contextual information in a non-social domain. Prior cultural psychology research has shown that people living in a collectivistic culture, such as Japan, are better at incorporating contextual information during perception of a focal object (e.g., relative condition) while people living in an individualistic culture, such as North America, are better at ignoring contextual information (e.g., absolute condition) when perceiving a focal object (Kitayama et al., 2003). These results suggest that cultural beliefs affect how a simple visual percept, such as a vertical line, is perceived and experienced.

Modulation of visual experience by cultural beliefs is thought to arise from frontal-parietal regions associated with high-level attentional modulation, rather than early stage primary perceptual processes associated with temporo-occipital regions (Hedden et al., 2008). Using fMRI, Hedden et al. (2008) measured neural activity while people completed a modified version of the FLT task. During scanning, people were asked to perform vertical line size judgments that involved either incorporating (relative condition) or ignoring (absolute) contextual information, such as the relationship between the perceived size of the line and the surrounding square frame. Brain imaging results showed that people recruited frontal and parietal regions associated with attentional control to a greater extent when engaged in a task that was incongruent with their cultural values. More specifically, neural activity in frontal-parietal regions increased when people of East Asian descent ignored contextual information and people of European descent incorporated contextual information during line size judgments. Moreover, degree of activation during the incongruent relative to the congruent judgments was negatively correlated with degree of individualism in people of European descent and degree of acculturation in people of East Asian descent. Hence, conscious perception of a vertical line embedded in a square frame and its underlying neural circuitry is affected by experience with and identification to a given cultural context.

Recent studies using ERP have found converging evidence of cultural values of individualism–collectivism on neural substrates of visual perception. In one study, Lewis et al. (2008) measured ERP while participants completed the oddball task, where they are shown visual stimuli in either a frequent or infrequent (i.e., oddball stimulus) manner. Results demonstrated that European-American participants showed greater novelty P3 amplitude for target events, whereas East Asians showed greater P3 amplitude to. In another study, Lin et al. (2008) recorded electrophysiological activity in extrastriate cortex while participants primed with either individualism or collectivism viewed compound visual stimuli in either a global or a local fashion. Results demonstrated that individualistic self-construal priming resulted in greater P1 amplitude during local relative to global processing, whereas collectivistic self-construal priming resulted in greater P1 amplitude during global relative to local processing. These results provide a novel demonstrate that temporarily heightening one's awareness of cultural values can dynamically alter neural responses during visual perception. Taken together, these findings provide convergent evidence that cultural values of individualism and collectivism modulate neural and electrophysiological responses during visual perception at both macro and micro timescales.

Memory

Cultural variation in holistic versus analytic thinking styles affects how people encode and retrieve information. Several cultural psychological studies have shown that Westerners are more likely to encode and retrieve focal objects in a complex visual scene, whereas East Asians encode focal and contextual information (Chua et al., 2005; Nisbett and Masuda, 2003; Nisbett et al., 2001). Recent cultural neuroscience evidence suggests that cultural variation in memory performance may occur, in part, to cultural variation in neural processing within lateral occipital regions, particularly in elderly populations (Gutchess et al., 2006; Goh et al., 2007). One cross-cultural neuroimaging study found that East Asians and Westerners vary within object-processing regions such as bilateral middle temporal gyrus (Gutchess et al., 2006). Another neuroimaging study comparing young and elderly East Asians and Westerners found that activity within the right lateral occipital region differed between East Asian and Western elderly, but not East Asian and Western young adults, providing novel evidence that neural regions may show cultural variation as a function of age (Goh et al., 2007).

Emotion

Culture shapes how people prefer to experience, express, recognize, and regulate their emotions (Mesquita and Leu, 2007). East Asian experience low arousal relative to high arousal positive emotions (Tsai, 2007), are more likely to suppress their emotions relative to Westerners (Butler et al., 2007). Additionally, both East Asians and Westerners demonstrate cultural specificity in emotion recognition, whereby they show greater recognition for emotions expressed by own cultural group members relative to members of other cultural groups (Elfenbein and Ambady, 2002). Recent cultural neuroscience of emotion research has shown cultural specificity effects

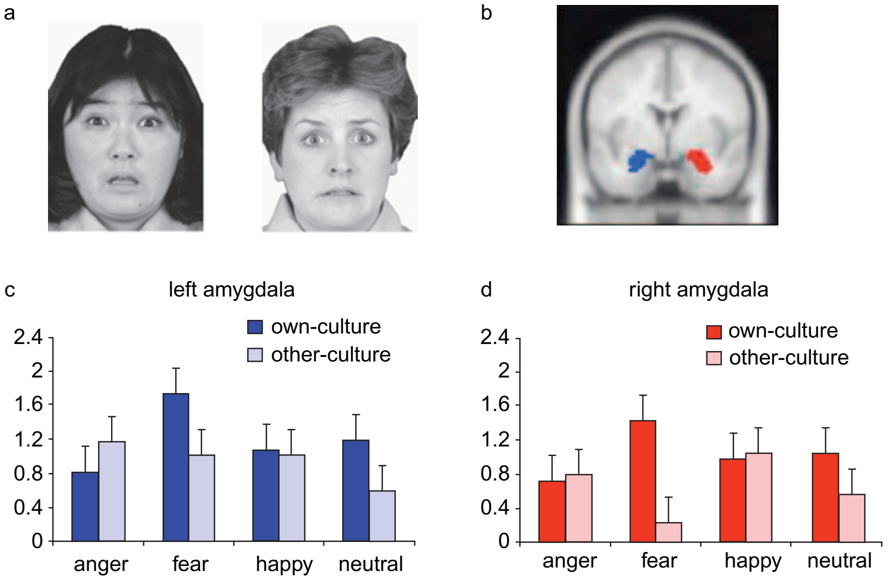

Fig. 4. Cultural specificity in bilateral amygdala response to fear faces (adapted with permission from Chiao et al., 2008b). (a) Examples of Japanese and Caucasian-American fear faces; (b) illustration of bilateral amygdala; participants show greater left (c) and right (d) amygdala response to fear expressed by members of one's own cultural group.

within a number of brain regions involved in emotion recognition. Consistent with prior behavioral findings, one recent study showed that both native Japanese and Caucasian-Americans exhibit greater amygdala response to fear faces expressed by own-relative to other-culture members (Chiao et al., 2008a, b, Fig. 4). Taken together, these findings provide convergent evidence that culture influences how people infer emotional states from nonverbal cues, and their underlying neural substrates, possibly by tuning neural responses toward familiar stimuli in the environment during development.

Another way that culture may affect affective neural response is by affecting its magnitude. Using cross-cultural neuroimaging, we have recently discovered a *cultural variation* effect in bilateral amygdala response to emotional scenes (Chiao et al., 2009c, in press). Caucasian-American (CA), Japanese-American (JA), and native Japanese (JP) participants, all of whom carried the S allele of the *5-HTTLPR* serotonin transporter gene, were studied using fMRI at 3T while they performed an emotion and cognitive inhibition task. Native Japanese S allele carriers showed significantly greater amygdala response relative to Japanese-American and Caucasian-American S allele carriers. Native Japanese S allele carriers showed significantly greater amygdala response relative to Japanese-American and Caucasian-American S allele carriers. Furthermore, there was no significant difference in amygdala response to emotional scenes between Japanese-American and Caucasian-American S allele carriers, suggesting that ethnicity of the participant is not a possible explanation for the difference between Native Japanese and Caucasian-American participants. By contrast to the emotion task, there was no significant main effect of cultural group in bilateral VLPFC response during inhibition. Our neuroimaging findings show that culture exerts a significant influence on bilateral amygdala response to emotional scenes, controlling for related genetic and racial factors.

Interpersonal perception

Recent cultural neuroscience evidence indicates that cultural group membership provides an important means by which people infer the mental states of others from nonverbal cues. The superior temporal sulcus (STS) is a region within the temporal lobe that transforms perceptual cues from the face, such as eye gaze direction and body orientation, into information about the goals and intentions of another (Nummenmaa and Calder, 2009). A recent neuroimaging study found that people exhibit STS activity when inferring the intentional states specifically from the eye region of others from their own-relative to other-culture (Adams et al., in press). These findings suggest that activity within STS processes culturally familiar percepts to a greater extent, possibly leading to greater mental state inference for own-relative to other-culture group members. Another recent study found that activity within the mesolimbic system responds more for culturally congruent dominant and submissive facial cues (Freeman et al., 2009). Individuals from egalitarian cultures, such as the United States, show greater mesolimbic response to dominant facial cues whereas individuals from hierarchical cultures, such as Japan, show greater mesolimbic response to submissive facial cues. Future research may examine whether cultural specificity in STS response results neural tuning within the lifespan toward familiar percepts, whether cultural values shape neural responses when forming first impressions of others from nonverbal cues as well as whether or not cultural reliance on display rules modulates cultural specificity or variation in response to nonverbal cues.

Social cognition

Cultural values, practices, and beliefs shape social behavior in profound ways. One of the most robust ways that values, such as individualism and collectivism, influence human behavior is in self-construal, or how people think about themselves in relation to others. Individualists think of themselves as autonomous form others, while collectivists think of themselves as highly interconnected with others (Markus and Kitayama, 1991; Triandis, 1995). Recent cultural neuroscience evidence indicates that neural substrates of self-knowledge and self-awareness are modulated by cultural values of individualism and collectivism (for review, see Chiao et al., 2008a). Evidence from social neuroscience indicates that specific brain regions, such as the medial prefrontal cortex (MPFC) and posterior cingulate cortex (PCC) are involved in self-evaluation and self-knowledge (Amodio and Frith, 2006). In one study, Caucasians, but not Chinese, showed greater neural activity within the MPFC during evaluation of personality traits of one's self relative to a close other (i.e., mother), suggesting cultural variation in MPFC response during self-evaluation (Zhu et al., 2007). More recent evidence has demonstrated that cultural values (i.e., individualism–collectivism), rather than cultural affiliation (i.e., East Asian–Westerners) per se, modulate neural response during self-evaluation. In one cross-cultural neuroimaging study, people in both Japan and the United States who endorsed individualistic values show greater MPFC activity for general relative to contextual self-descriptions, whereas people who endorsed collectivistic values show greater MPFC for contextual relative to general self-descriptions (Chiao et al., 2009a, Fig. 5). Supporting this view, another study using cultural priming showed that even temporarily heightening awareness of individualistic and collectivistic values in bicultural individuals (i.e., Asian-Americans) modulates MPFC and PCC in a similar manner (Chiao et al., 2009b, Fig. 6). Taken together, these studies provide convergent evidence that cultural values of individualism–collectivism shape neural representations of self-knowledge.

Additionally, cultural values of individualism and collectivism can moderate neural mechanisms underlying self-awareness. In a recent neuroimaging study examining self-construal style and neural correlates of self-awareness, Sui and Han (2007) primed participants with either an individualistic or a collectivistic self-construal style and then presented them with facial images of themselves, a familiar other or a scrambled face. Once the facial image was presented, participants were asked to indicate the head orientation of the intact face or the location of a gray bar next to the scrambled face. Greater activation within the middle frontal cortex was found for self relative to familiar and scrambled faces in the individualistic prime group while greater activation within the middle frontal cortex was found for both self and

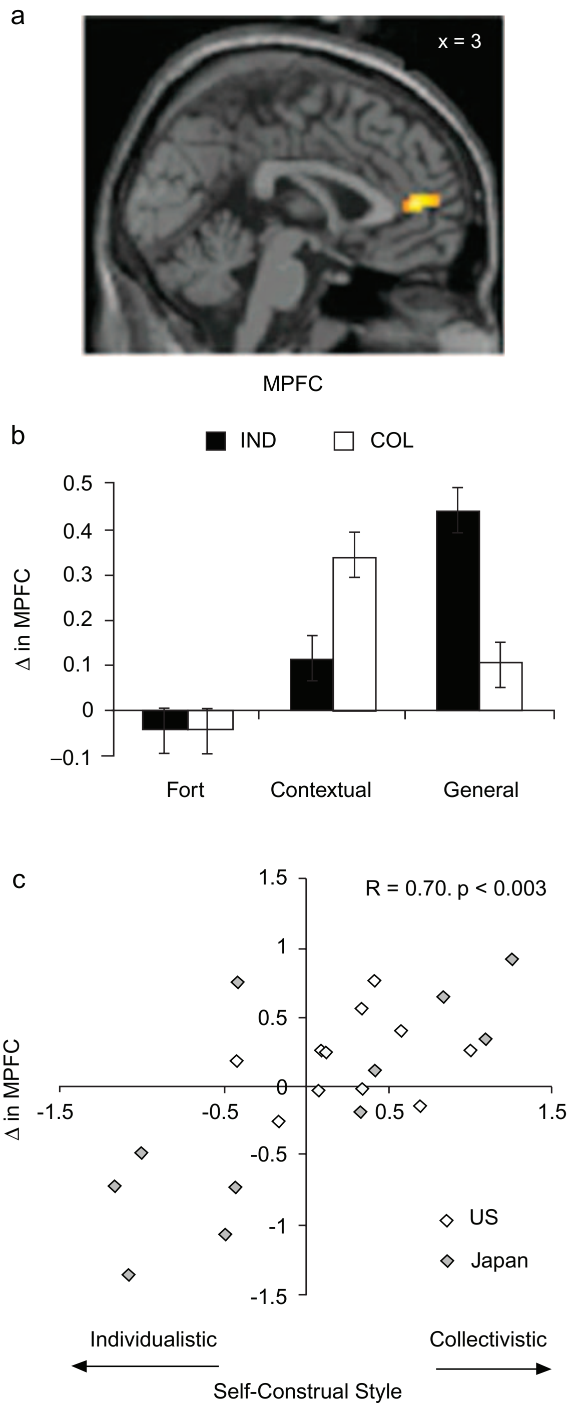

Fig. 5. Neural basis of individualistic and collectivistic views of self (adapted with permission from Chiao et al., 2009a). (a) Cultural values of individualism and collectivism modulate activity within medial prefrontal cortex (MPFC). (b) In both the United States and Japan, participants who endorse individualistic cultural values show greater MPFC response to general relative to contextual self-descriptions. Participants who endorse collectivistic cultural values show greater MPFC response to contextual relative to general self-descriptions. (c) Irrespective of nationality, the degree to which a person endorses individualistic or collectivistic values is positively correlated with neural activity within MPFC to general relative to contextual self-descriptions, respectively.

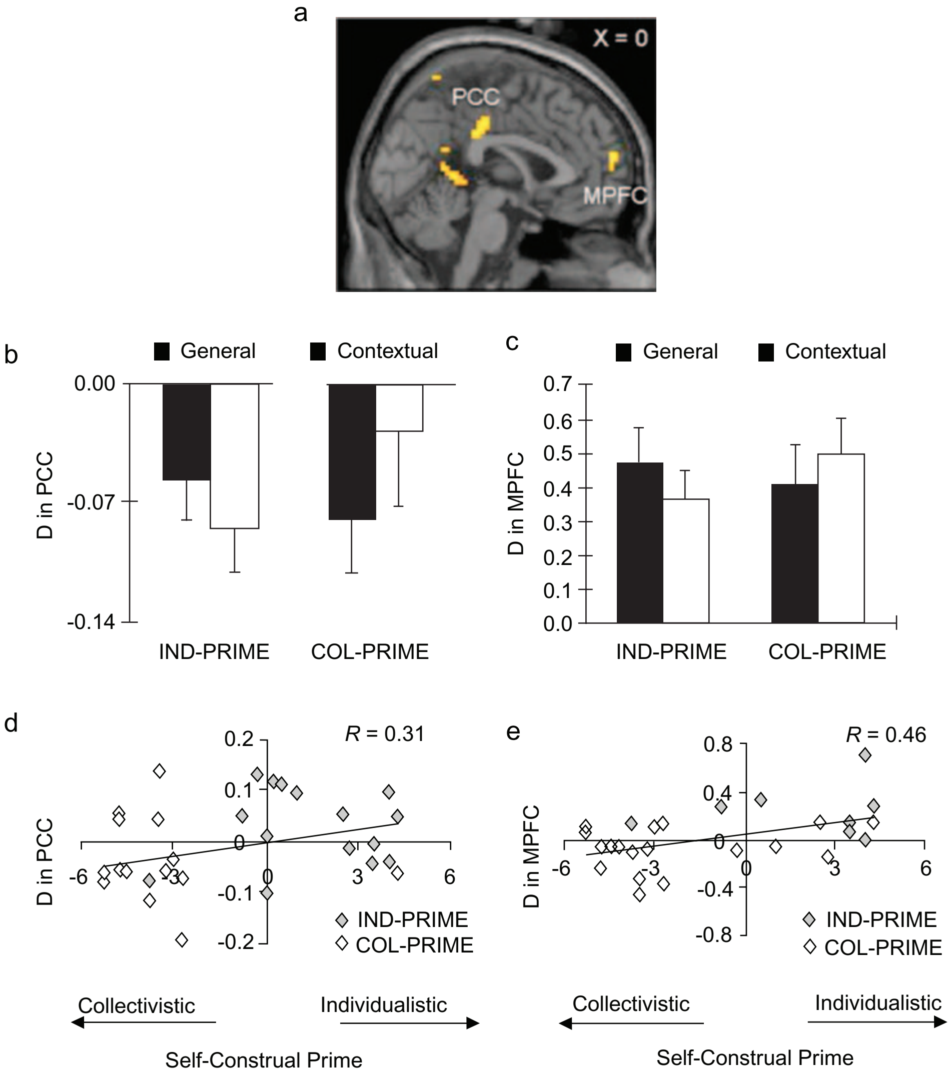

Fig. 6. Dynamic cultural influences on neural representations of self (adapted with permission from Chiao et al., 2009b). (a) Modulation of neural activity within cortical midline structures, including the posterior cingulate cortex (PCC) and medial prefrontal cortex (MPFC) as a function of cultural priming. Bicultural participants primed with individualistic cultural values show greater PCC (b) and MPFC (c) to general relative to contextual self-descriptions. Bicultural participants primed with collectivistic cultural values show greater PCC (b) and MPFC (c) response to contextual relative to general self-descriptions. The degree to which a person is primed with individualistic or collectivistic values is positively correlated with neural activity within PCC (d) and MPFC (e) to general relative to contextual self-descriptions, respectively.

familiar faces relative to scrambled faces in the collectivistic prime group. This modulation of neural activity by self-construal style was not present in other brain regions activated during the task, such as the right fusiform gyrus, a region critical to face processing. Hence, these results highlight the influence of cultural values on neural activity during self-awareness.

Finally, religious beliefs also play an important role in modulating neural responses underlying social cognition. One set of neuroimaging studies examining the neural substrates of religiosity found activity within theory-of-mind regions, including left precuneus, left temporoparietal junction, and left middle frontal gyrus was correlated with the degree of one's religiosity (Kapogiannis et al., 2009). Additionally, religious practices, such as praying, also modulate neural responses within theory of mind regions. For instance, compared to formalized prayer and secular cognition, improvised praying activated the temporopolar region, MPFC, temporoparietal junction, and precuneus (Schjoedt et al., 2009). Finally, religious beliefs affect neural representations of the self. Whereas atheists typically recruit ventral MPFC during self-evaluation, religious individuals show greater response within dorsal MPFC, suggesting that religious beliefs promote greater evaluation, rather than representation, of one's self (Han et al., 2008). Hence, the human ability to possess religious beliefs and exercise religious practices relies on theory-of-mind and mentalizing brain regions that facilitate the representation and evaluation of own and others (e.g., human, God) mental states.

Implications of cultural neuroscience for basic and applied research

It is not expected that the study of all psychological and biological phenomena will necessitate a cultural neuroscience approach. Rather, the goal and challenge for cultural neuroscience is to identify the phenomena that can be readily mapped within and across multiple levels of analysis. There are at least three foreseeable benefits of a cultural neuroscience approach for basic and applied research: (1) merging the social and natural sciences, (2) informing interethnic ideology, and (3) enhancing the condition and care of human health across diverse cultural populations.

Merging the scientific study of culture and biology

The increasing stratification of the social and natural sciences within universities and academic subfields has led to deep conceptual and methodological schisms between different communities of researchers. In an influential lecture, Snow, an influential British physicist and novelist (1959), once famously characterized the fissure between social and natural sciences as "the two cultures." Even within the field of anthropology, which Boas originally envisioned as simultaneously encompassing cultural and social anthropology, physical and biological anthropology, archaeology, and linguistics, there has historically been such deep intrafield antagonism, that some anthropology departments within the American universities have even split into two, with one-half of the department focused on cultural approaches, while the other half focused on biological approaches to the same questions (Shenk, 2006). Is the gap between cultural and biological sciences too wide to be bridged within a single discipline? How might consilience be achieved (Wilson, 1998)? Remarkably, anthropology is currently witnessing a rebirth of unification within its disparate branches through the emergence of neuroanthropology (Brown and Seligman, in press; Dominguez Duque et al., in press; Rilling, 2009; Seligman and Brown, in press). Akin to its sister field, psychology as a hub science (Cacioppo, 2007) stands in a natural position to merge the scientific study of culture and biology by harnessing theories and methods from every area of psychology, from evolutionary and cognitive to cultural and developmental. The empirical tools needed to investigate the links across multiple levels of analysis are available now in ways not previously imaginable. The cultural neuroscience framework represents an opportunity to transcend the confines of academic subfields and address age-old questions regarding the mutual constitution of cultural and biological influences on human behavior in novel ways.

Informing interethnic ideology

Research in cultural neuroscience may also inform public policy issues related to cultural diversity and interethnic justice. As a result of globalization, cultural communities of the world are becoming increasingly interdependent and interethnic, leading to an increasing urgency to understand how diverse communities of people may optimally coexist (Bodenhausen, in press;

Wolsko et al., 2000). On the one hand, interethnic ideologies such as colorblindness advocate treating people of different cultural heritages similarly, with no regard to interethnic differences. On the other hand, interethnic ideologies such as pluralism advocate embracing cultural differences and creating public policies that respect interethnic differences. Research in cultural neuroscience can potentially inform this important debate by studying how cultural identity affects the brain and behavior, whether or not cultural traits have adaptive value and how changes in cultural diversity may affect the human mind, brain, and behavior. At the same time, scientific rigor and ethical care is needed when seeking to apply cultural neuroscience evidence toward larger public policy discourse regarding how best to achieve optimal coexistence of diverse cultural and ethnic groups.

Implications for population health

Finally, the important interplay of culture and genes in the study of population health has long been acknowledged (Shields et al., 2005; Wang and Sue, 2005). For instance, whereas Ashkenazi Jews have a greater likelihood of Tay-Sachs disease, people from Northern Europe are more likely to develop cystic fibrosis (Exner et al., 2001; Wang and Sue, 2005). Another example of population differences in health as a function of differences in allelic frequency is the gene *CYP2A6* and nicotine addiction (Shields et al., 2005). Protective forms of the *CYP2A6* gene are very rare in Europeans and Africans (~3%), but more prevalent in Japanese and Koreans (~24%) (Shields et al., 2005). Cross-national epidemiological studies, including the 2008 World Health Organization cross-national survey of affective disorders, indicates significant variation in global prevalence of mental health disorders, such as anxiety and major depression (Kessler and Ustun, 2008; Weissman et al., 1996). How do differences in genetic frequencies affect brain systems and behavior underlying physical and mental health conditions? How do cultural factors influence the expression and function of these genes and their regulatory effects on brain and behavior?

The answers to these intriguing questions are finally within our empirical grasp. By using the cultural neuroscience framework to identify and investigate candidate phenomena using the multiple levels of analysis approach, we will enhance our chances of understanding how sociocultural and biological forces interact and shape each other as well as find potential ways to direct this knowledge toward timely issues in population health.

Cultural neuroscience as a once and future discipline

The beginning of the 20th century marked the formal birth of the study of culture, with the emergence of the field of anthropology and with cultural psychology joining forces with anthropology toward the latter half of the century. It is humbling to note that more than 100 years have since passed and scientists are still asking the same questions as Boas in 1907. Why does cultural diversity exist and what are its origins? Yet, it is encouraging to observe that the beginning of the 21st century marks the reunification of the study of culture and biology with the emergence of the field of cultural neuroscience. As challenges of living in an increasingly globalized and interethnic world increase, cultural neuroscience as a once and future discipline represents a necessary moment in the history of psychology and neuroscience, one that offers scientists with a fresh opportunity to transcend traditional academic confines and direct their intellectual prowess toward solving elusive, timeless questions on the nature and origins of human diversity. Whether or not it will take a century to pass before we gain a clearer grasp of how culture emerges from human biology and how human biology shapes culture remains to be seen.

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Subject Index