Behavioral Oscillations in Verification of Relational Role Bindings

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Abstract

Human understanding of relations between objects depends on the ability to code meaningful role bindings. Computational models of relational reasoning have proposed that neural oscillations provide a basic mechanism enabling working memory to code the bindings of objects into relational roles. We adapted a behavioral oscillation paradigm to investigate moment-to-moment changes in representations of semantic roles. On each trial, a picture was presented showing an action (chasing) relating two animals, one animal playing an agent role (chaser) and the other playing a patient role (chased). After the picture disappeared, the inter-stimulus interval (ISI) was varied in densely-sampled increments followed by a verbal probe indicating an animal in a role. Reaction time (RT) to decide the validity of the verbal probe was recorded. We found that RTs varied systematically with ISI in an oscillatory fashion. A task that required memory for a relational role evoked stronger theta- and alpha-band oscillations than did a memory task not involving relational roles. The behavioral oscillation patterns in the role-identification task revealed a phase shift between the two semantic roles in the alpha band.

Keywords: behavioral oscillation; neural oscillation; propositional representation; relations; binding.

Introduction

In order to reason with structured propositions, human working memory requires some mechanism to solve the *binding problem*: keeping track of "who is doing what to whom." For example, the proposition *lion chases leopard* must be distinguished from *leopard chases lion*. Although both propositions are composed of the same elements (i.e., same objects and action), their different meanings alter judgments of which animal is more aggressive. In other words, the inference depends on which animal is bound to which role (*chaser* or *chased*).

Solving the binding problem is trivial for symbolic systems that encode propositions in predicate-calculus style, marking roles by position in a structured list. For example, *lion chases leopard* could be represented simply as *chase (lion, leopard)*, where the order of elements signifies that lion is bound to the *chaser* role and leopard to the *chased* role. However, list position is not a plausible mechanism for coding role bindings within a neural system. For a neural representation, the binding problem poses the threat of *catastrophic superimposition* (von der Malsburg, 1985): jointly activating a distributed set of neurons for each element of a proposition will not distinguish the roles filled by different objects, or even distinguish multiple objects as separate entities.

One potential solution to the binding problem within a neural system exploits the informational capacity of *time* as a dimension of neural activity. Neural oscillations can code role bindings by having pools of neurons respectively representing a role and an object fire in synchrony if they are bound together and out of synchrony if not (von der Malsburg & Buhmann, 1992). Temporal structure in the form of oscillations is prominent in the brain (Uhlhaas et al., 2009).

Although no direct evidence connects such oscillations to the coding of propositions, there is evidence that oscillatory neural activity supports a variety of cognitive processes. Findings from numerous electroencephalography (EEG) and magnetoencephalography (MEG) studies have implicated alpha-band rhythms (approximately 10 Hz) in selective visual attention (e.g., Händel, Haarmeier & Jensen, 2011; Song et al., 2014). One general theoretical proposal is that alpha-band oscillations are related to the timing of inhibitory processes that support controlled knowledge access (Klimesch, 2012; Klimesch, Sauseng & Hansimayr, 2007).

EEG evidence also suggests that phase synchrony within the frontoparietal network can bind object properties together in working memory (Philips, Takeda & Singh, 2012). Synchronous activity within local neural circuits tends to occur in the high-frequency gamma band (>30 Hz), whereas entrainment of neural activity across brain regions occurs at the lower theta band (4-8 Hz) (Canolty & Knight, 2010). Through *cross-frequency coupling* (Jensen & Colgin, 2007), the phase of theta oscillations modulates the power of the gamma band. Long-distance communication between brain areas involved in coding propositions (e.g., the prefrontal cortex and posterior regions that code semantic representations of object concepts) could be facilitated by cross-frequency coupling (Knowlton, Morrison, Hummel, & Holyoak, 2012). Several computational models of relational reasoning and cognitive control have employed neural oscillations as a basic mechanism enabling working memory to code the bindings of objects into relational roles (Doumas, Hummel & Sandhofer, 2008; Hummel & Holyoak, 1997, 2003; Shastri & Ajjanagadde, 1993; Verguts, 2017).

Behavioral paradigms that tap into oscillatory phenomena may provide indirect evidence of neural oscillatory patterns. Several previous studies have demonstrated the rhythmic nature of perceptual processes based on psychophysical measurements of response time and accuracy (for a review see VanRullen & Dubois, 2011). For example, Lu, Morrison, Hummel and Holyoak (2006) showed that visual information presented as temporal flicker in the gamma band can modulate the perception of spatial relations between multiple objects in a subsequent display. Other studies have revealed stimulus-locked fluctuations in behavioral performance elicited by rhythmic brain activity (Desimone & Duncan, 1995). Such behavioral oscillations have been observed in studies of attention and visual search (e.g, Dugué, Marque & VanRullen, 2015; Huang, Chen & Luo, 2015; Song et al., 2014), as well as multisensory integration (e.g., Fiebelkorn et al., 2011) and visual categorization (e.g., Drewes, Zhu, Wutz & Melcher, 2015).

In the current study, we created a behavioral paradigm to determine whether behavioral oscillations can provide insight into the neural code for a proposition in working memory. In general terms, the task required matching relational roles presented in a picture to verbal probes. By using different modes (visual and verbal) to present stimuli and probes, we ensured that the representations used to perform the task were intermodal in nature. We aimed to answer two basic questions: (1) is the mental processing of distinct roles in a relation reflected in behavioral oscillations (specifically, in periodicities in reaction time); and (2) if so, what frequency components are involved? Although our behavioral paradigm does not provide the temporal resolution necessary to detect very high-frequency oscillations (gamma band), it could potentially reveal oscillations and phase-differences at slower frequencies, such as the alpha and theta bands.

Experiment 1

The goal of Experiment 1 was to examining whether oscillatory behavioral patterns could be revealed when participants make explicit role-binding judgments (deciding whether or not a named animal filled a specified role).

Methods

Participants

Thirty-six participants (mean age = 20.7 years; 31 female) were recruited from the University of California, Los Angeles (UCLA) Psychology Department subject pool. All participants had normal or corrected-to-normal vision. Participants provided written consent via a preliminary online survey in accordance with the UCLA Institutional Review Board and were compensated with course credit.

Stimuli

A set of 38 animal images was constructed by manually drawing each animal as a black-and-white line drawing. Using this set of individual animals, 28 pairs of animals were selected and used to generate pictures in which one animal was chasing the other (see Figure 1). One animal could appear in more than one pair. Paired animals were used to create four different pictures, so that each animal was depicted equally often in the *chaser* (agent) and *chased* (patient) roles. The left/right positions and facing directions of the chaser and chased were randomly assigned on each trial to avoid potential biases due to the habit of scanning from left to right. To ensure all versions of the pictures depicted plausible *chasing* relations, paired animals were selected to have similar values on scales of rated fierceness and size of animals (Holyoak & Mah, 1981).

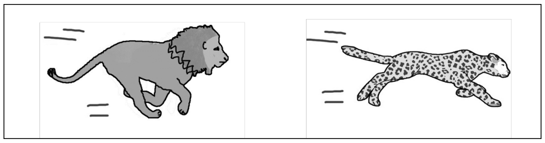

Figure 1. Example of a picture of an animal pair used in the experiments.

Procedure

The experiment was created in Matlab with Psychtoolbox (Brainard & Vision, 1997). Stimuli were presented on a 1024×768 monitor with a refresh rate of 90 Hz. The experiment was administered in two sessions. In order to minimize RT variability due to difficulties in perceptual encoding, at the beginning of the first session participants were familiarized with the pictures of individual animals to be used in the main task. On each trial in this familiarization phase, a picture of a single animal was presented with four animal names below it. Participants were asked to click on the name of the animal in the picture, after which they received feedback. If they clicked on a wrong animal name, the trial was repeated at the end of the session. This stage continued until they clicked all animal names correctly.

After the familiarization phase, the main experimental task was presented, which involved making judgments about relational roles (*chaser* vs. *chased*). On each trial, a fixation cross was presented for 500 ms, after which a picture of one animal chasing another was presented for 3 s (see Figure 1). The picture then disappeared, and the ISI was varied from 100 ms to 1000 ms with a step size of 33.3 ms, yielding a total of 28 ISIs.

After the appropriate ISI on a trial, a verbal test probe appeared. The probe showed the name of either the *chaser* or the *chased* animal on that trial, colored in either red or green. Participants were instructed (at the beginning of the main task) that if the word appeared in red, the probe was asking if the animal was the *chaser* in the picture. If the word appeared in green, the probe was asking if the animal was the one *chased*. For example, if the word *lion* appeared in red, the probe was to be interpreted as *lion is chaser*. Participants quickly learned the color code, which was intended to make the probe as compact as possible so that perceptual processing time would be minimal. Participants were asked to indicate whether the probe was true by pressing the *up arrow* key for “true” and the *down arrow* key for “false” (avoid any confounding with the left/right spatial locations and orientations of pictured animals). RTs were measured after each trial (see Figure 2).

Before beginning the main task, participants received practice trials using pairs of human figures (women and men, girls and boys). Participants completed at least two practice blocks, each of which included 12 trials. If participants did not complete these two initial blocks with at least 83% accuracy (i.e., correct on 10 out of 12 trials), they received additional practice blocks until they completed two consecutive blocks of practice trials with minimum accuracy of 83%.

After the practice trials, participants performed the main task, in which animal figures were used to generate the picture pairs. Animal pairs were pseudo-randomly selected for each trial, and the total number of presentations of each animal pair was equated. A total of 336 trials were presented in one session (*chaser*/*chased* * true/false * 28 ISIs * 3 repetitions), yielding a total of 672 trials over the two sessions. Each session took around 40 minutes, with the two separated by 1-7 days. The familiarization phase and practice trials were only given in the first session.

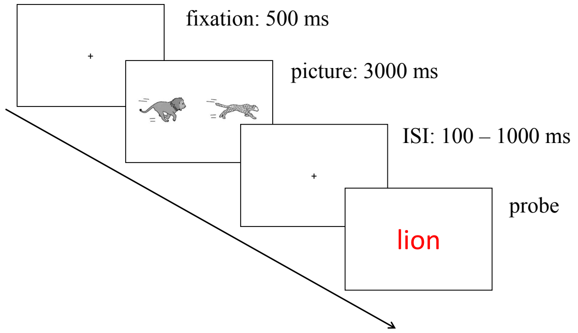

Figure 2. The basic procedure on a trial in Experiment 1. After a fixation cross, a picture showing one animal chasing another was presented for 3 s. Following an ISI varying from 100 ms to 1000 ms, a probe (animal name in red or green) was presented. The participant then pressed a key to respond “true” or “false”.

Results and Discussion

Data from two out of 36 subjects were discarded because overall accuracy was more than 2 SD lower than mean accuracy across all participants ($M = .95$, $SD = 0.08$). Trials with response times that were outside the range of ± 2 SD mean RT ($M = 1035$ ms, $SD = 217$ ms), or that yielded incorrect responses, were removed from data analysis. These criteria resulted in exclusion of about 5% of the total data.

RTs were then averaged across participants for each of the four conditions (see Figure 3): relational roles (*chaser* vs. *chased*) × probe validity (true vs. false). A two-way ANOVA revealed a significant interaction between the two variables, $F(1, 33) = 33.71$, $p < .001$, $\eta_p^2 = 1.0$, as well as significant main effects of both role, $F(1, 33) = 20.35$, $p < .001$, $\eta_p^2 = 0.992$, and validity, $F(1, 33) = 23.05$, $p < .001$, $\eta_p^2 = 0.997$. For the *chaser* role, responses were reliably faster for true than for false trials, $F(1, 33) = 45.26$, $p < .001$, $\eta_p^2 = 1.0$. In contrast, for the *chased* role true trials yielded longer RTs than false trials, $F(1, 33) = 791.42$, $p < .001$, $\eta_p^2 = 1.0$.

The interaction between role and validity suggests that in representing the depicted proposition, participants may have focused on the object in the agent role, coding it both as the filler of the agent role and as *not* the filler of the patient role. For example, given a picture of a lion chasing a leopard, the participant might represent not only *lion is chaser* and *leopard is chased* but also *not (lion is chased)*. The latter representation would provide an additional means of rejecting a false statement about the object role (e.g., a probe indicating *lion is chased*), so that RTs for queries about the object were faster when the probe was false rather than true. A second possibility is that the *up* and *down* arrow keys were preferentially associated with high-dominance (i.e., *chaser*) and low-dominance (i.e., *chased*) semantic roles, respectively (Casasanto & Bottini, 2014). For the *chased* condition, pressing the *up* arrow on true trials may have yielded slow responses due to conflict between vertical space and valence.

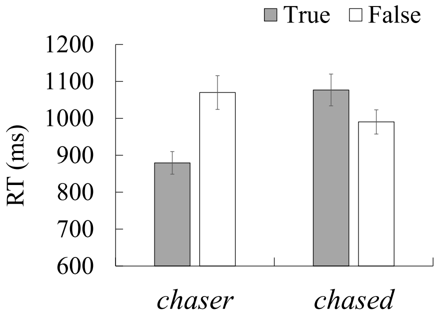

Figure 3. Mean RTs for true and false probes for agent (*chaser*) and patient (*chased*) roles (Experiment 1).

We then analyzed the frequency components underlying the change of RTs as a function of ISIs to determine whether any behavioral oscillations could be identified. Because responses to false probes appeared to involve multiple strategies, we confined these analyses to trials with true probes. RTs were averaged within participants for each role condition for each of the 28 ISIs. In preprocessing, data were first detrended (see Figure 4). The trend of the data was calculated by fitting a linear regression with a sliding window of 300 ms in 33-ms increments across the entire range of ISIs. Temporal filtering was performed on the data with a Hanning window filter to attenuate the extremely low frequency largely driven by the performance with the shortest and longest ISI. The filtering operation was performed separately for each condition. Data were zero-padded by adding 38 zero points after the RT temporal profile to yield less noisy outputs from the frequency analysis.

We conducted spectrum analysis using a fast Fourier transformation (FFT) for each participant in each condition to calculate the power of frequencies embedded in the RT time-series data. To assess statistical reliability, permutation tests were conducted by randomly shuffling each participant’s time-series data and conducting FFT analyses based on the shuffled data. FFT results for shuffled data reveal the frequency distribution generated by random noise. By repeating this procedure 10,000 times for each condition of each participant, a distribution of spectral power for each frequency point was obtained. We calculated the $p < .05$

(uncorrected) thresholds for each frequency. If the FFT amplitude of a frequency in the true signal passes the permutation line, then this frequency in the true signal is unlikely to have been generated from random noise (for details of permutation tests see Huang et al., 2015).

As depicted in Figure 4 (right), these analyses revealed that true RTs for the *chaser* probe showed reliable oscillations within the ranges of 3-5 Hz and 11-13 Hz. True *chased* probes evoked oscillations within the ranges of 3-6 Hz and 9-13 Hz. Considered together, both *chaser* and *chased* probes evoked both 4-5 Hz (theta-band) and 10-12 Hz (alpha-band) oscillations in RTs.

To investigate the temporal relation in representing true *chaser* and *chased* probes, the phase difference between the true *chaser* and *chased* conditions for each participant was calculated within the range of frequencies that passed the permutation tests for either condition. Figure 5 presents a histogram of phase shifts across participants. The statistic tests were conducted using the CircStat toolbox (Berens, 2009). At a frequency of 10 Hz (alpha band) in behavioral oscillations, a reliable phase difference was observed between the true *chaser* versus *chased* probes (one-sample test for the mean angle, M = 88.24, 95% CI [35.5, 140.9], Raleigh test, $p = 0.05$) (see Figure 5).

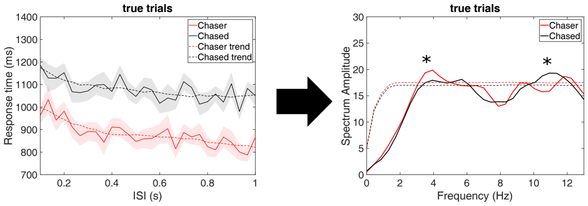

Figure 4. Behavioral oscillations observed in Experiment 1. Left, raw RT data as a function of ISIs (left) with dashed lines indicating the trend. Right, after detrending the RT data, the spectrum analysis revealed frequency amplitudes for true *chased* and *chaser* probes, showing significant oscillation frequencies in both 3-6 Hz (theta-band) and 9-13 Hz (alpha-band).

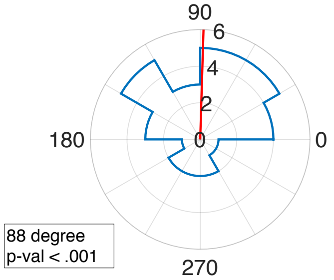

Figure 5. Phase shift observed in Experiment 1. Histogram of phase shifts for true probes (RTs for *chaser* – *chased*) across participants, with a mean shift of 88 degrees at mean phase angle of 10 Hz.

Experiment 2

The results of Experiment 1 revealed behavioral oscillations in RTs, with a systematic phase shift in the alpha frequency band between the agent and patient roles of a proposition. This finding is consistent with computational models in which relational roles are kept distinct in working memory by phase shifts. However, an alternative possibility is that the phase shift simply reflects alternating attention to the two objects in the picture, regardless of their roles in the proposition.

To evaluate this alternative account, in Experiment 2 we used the same basic materials, but altered the task so that relational roles were irrelevant. If the out-of-phase oscillation in RT observed in Experiment 1 reflected linked representations for different relational roles, then no such phase shift should be found when the roles are rendered irrelevant to the required task.

Methods

Participants

Thirty-three participants (mean age = 20.79 years; 14 female) were recruited from the UCLA Psychology Department subject pool. All participants had normal or corrected-to-normal vision. Participants provided written consent via a preliminary online survey in accordance with the UCLA Institutional Review Board and were compensated with course credit.

Stimuli and Procedure

The picture set was identical to that used in Experiment 1, and the basic procedure was very similar except that the binary response required in Experiment 2 was "yes/no" rather than "true/false". The probe was again an animal name, but now always presented in red font. The animal name could be one of the two animals in the picture or an irrelevant animal name. The irrelevant name was randomly chosen from the list of animal names, excluding the two animals in the picture. The task was to decide whether the probe named an animal presented in the immediately-preceding picture. For example, if the picture had shown a lion chasing a leopard, the correct response would be "yes" if the probe word was either *lion* or *leopard*, but "no" if the probe was *tiger.* Because all animals were used repeatedly within the experiment, reliable recognition judgments could not be based on familiarity, but rather would require recollection of the specific animals shown in the immediately-preceding picture (see Yonelinas, 2002).

Results and Discussion

The same criterion for removing trials that was used in Experiment 1 was also applied in Experiment 2. The mean proportion correct overall was .95 (SD = 0.03) and the mean RT overall was 760 ms (SD = 165 ms). Our criteria resulted in exclusion of about 6.5% of the total data.

Although the roles (*chaser* vs. *chased*) were irrelevant to the yes/no recognition decision, "yes" probes can be categorized according to the role played by the animal. A *t*-test revealed that "yes" responses to *chaser* animals (*M* = 707 ms, *SD* = 149 ms) were slightly but reliably faster than responses to *chased* animals (*M* = 723 ms, *SD* = 157 ms), $t(33) = 3.33$, $p = .002$. This finding suggests that participants automatically processed the relation shown in the picture even though it was not relevant to the recognition task. The RT advantage for the *chaser* over the *chased* animal supports the hypothesis (discussed in connection with Experiment 1) that participants tended to focus greater attention on the animal in the agent role. RTs for "no" trials (M = 740 ms, SD = 154 ms) were significantly longer than overall RTs for "yes" trials (M = 715 ms, SD = 153 ms), $t(33) = 2.32$, p = 0.027.

FFT analysis of "yes" probes yielded similar frequency components but weaker spectrum amplitudes compared to true probes in Experiment 1. As shown in Figure 6 (right), the spectrum amplitudes in the yes/no task were about half of those observed amplitudes in the role-judgment task. RTs for the *chaser* animal evoked reliable oscillations within the range of 3-5 Hz and 10-12 Hz, while RTs for the *chased* animal evoked reliable oscillations within the range of 4-6 Hz and 10-12 Hz. Taken together, the "yes" probes evoked theta- and alpha-band oscillations similar to those evoked by the true probes in Experiment 1; however, the amplitudes of these oscillations were much weaker in the yes/no recognition task (Experiment 2) compared to the role-judgment task (Experiment 1).

An analysis of possible phase shifts was performed in the same manner as in Experiment 1. Critically, no reliable phase differences were found at any frequency between RTs to the *chaser* vs. *chased* animal. Accordingly, the out-of-phase oscillations observed in Experiment 1 can be interpreted as evidence that phase shifts serve to code relational roles in working memory, and do not simply reflect variations in attention to the two animals.

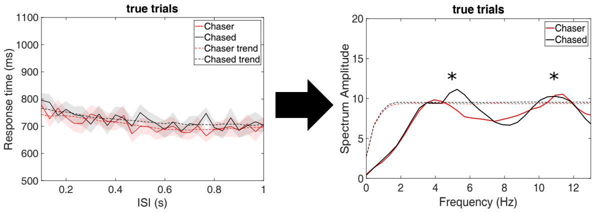

Figure 6. Raw data (left) and corresponding frequency amplitudes after detrending (right) for "yes" probes involving the animal in the *chaser* or else *chased* role (Experiment 2).

General Discussion

The present study provides the first behavioral evidence that oscillations may underlie the representation of a proposition in working memory. After seeing a picture of one animal chasing another, participants in Experiment 1 responded to a verbal probe (word in a colored font) indicating that a particular animal was in a specific semantic role (*chaser* or *chased*). Using a densely-sampled ISI in the range of 100 ms to 1000 ms, we found that RTs to decide whether the stated role assignment was true or false yielded behavioral oscillations. Specifically, RTs to true probes oscillated in the theta band (approximately 4-5 Hz) and also the faster alpha band (10-12 Hz). Moreover, in the alpha band a mean phase shift of about 90 degrees separated the oscillations of the two roles. RTs were faster overall to probes involving the animal in the *chaser* role (for false as well as true probes), suggesting that participants focused greater attention on the animal in the agent role.

In Experiment 2, participants performed a yes/no recognition task, deciding whether or not a named animal had appeared in the picture, regardless of role. Behavioral oscillations were observed in the same frequency bands as in Experiment 1, but with greatly reduced amplitudes. Critically, when the semantic roles were irrelevant to the decision (Experiment 2), no phase shift was observed between probes involving the two roles. Taken together, these findings suggest that phase shifts in behavioral alpha-band oscillations reflect the neural code for dynamic bindings of entities into relational roles to form a proposition.

The present findings are preliminary, and any interpretation in terms of neurocomputational mechanisms must be tentative. The phase shift observed in the alpha band when making judgments about semantic roles (Experiment 1) might reflect inhibitory processes that aid in focusing attention on one of the two roles by momentarily suppressing the other (Knowlton et al., 2012). The theta-band oscillations may reflect some type of cross-frequency coupling. As Klimesch (2012) has noted, harmonic frequencies are expected to optimize between-frequency communication (also see Palva & Palva, 2007). The faster alpha frequency (10 Hz) at which oscillations were observed in the present study is a harmonic of the slower theta frequency (5 Hz) that was also observed, as is the yet faster frequency typically associated with the gamma band (40 Hz). Oscillations at the latter frequency would be too fast to be detectable by the behavioral paradigm employed here. In general, the present findings provide support for neurocomputational models that posit neural oscillations as a code for relational role bindings held in working memory (Knowlton et al., 2012).

Several limitations of the current study should be addressed in future studies. We found that the amplitude of RT oscillations in Experiment 2 (yes/no recognition task) was smaller than that observed for Experiment 1 (true/false binding task). This amplitude difference may have resulted from the difference in overall task difficulty between the two experiments, and/or from the greater involvement of semantic role representations in Experiment 1. Similarly, we cannot rule out the possibility that the difference in phase shifts between the experiments reflected differential demands on attention or memory retrieval. Future studies should aim to address these issues, and also explore the possibility that behavioral oscillations may be detectable in reasoning tasks that require integration of multiple relations (e.g., Waltz et al., 1999). Although definitive evidence regarding the neural code for thought must await advances in neuroimaging technology, behavioral evidence may be able to help refine hypotheses about what form this code may take.

Acknowledgments

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