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Calories count: Memory of eating is evolutionarily special

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ABSTRACT

How well do we remember eating food? Some nutritional scientists have decried memory of eating as being highly unreliable (i.e. low in accuracy), but it is unclear if memory of eating is particularly worse than memory of other behaviors. In fact, evolutionary reasoning suggests the mammalian memory system might be biased towards enhanced memory of eating. We created a novel behavioral task to investigate the relative strength and determinants of memory of eating. In this task, participants were cued to eat a single item of food every time a tone was sounded and were later asked to recall how many items of food they consumed. In Experiment 1, we found that memory for the behavior of eating was more accurate than memory for similar but noneating behaviors. In Experiment 2, we ruled out a potential physiological mechanism (glucose ingestion) behind this effect. Last, in two pre-registered studies, we explored determinants of memory of eating. In Experiment 3, we found that the caloric density of the consumed food item potentiates its ability to be remembered and in Experiment 4 we found that a slow eating rate results in more accurate memory of eating than a fast eating rate. Understanding these and future factors that influence memory of eating might be useful in designing intervention strategies to enhance memory of eating, which has been shown to reduce future food consumption. Ultimately these four studies inform our understanding of how selective pressures shaped memory and lay the groundwork for further investigations into memory of eating.

> *"Our stomachs are bad at math, and what's more, we get no help from our attention or our memory. We don't register how many pieces of candy we had from the communal candy dish at work, and whether we ate 20 French fries or 30. It gets even worse when we're out dining with our friends and family. Five minutes after dinner, 31 percent of the people leaving an Italian restaurant couldn't even remember how much bread they ate, and 12 percent of the bread eaters denied having eaten any bread at all."* – Wansink (2006)

The quote above is from Brian Wansink's *Mindless Eating.* We now know the integrity of these data is shaky at best (Lee, 2018; van der Zee, 2017)—but the idea raised here is interesting: how well do we remember eating? A number of studies (e.g., Armstrong et al., 2000; Baxter, Thompson, Litaker, Frye, & Guinn, 2002; Fries, Green, & Bowen, 1995) appear to support Wansink's claim and show that participants often underestimate how much food they consumed 24-hours prior. This proclivity to underestimate consumption has led some in the nutritional and medical communities to proclaim that self-reported dietary assessment techniques "offer an inadequate basis for scientific conclusions" (Archer, Marlow, & Lavie, 2018; Schoeller et al., 2013). It remains unclear however, if this underestimation bias in memory is unique to eating behavior, as it may be the case that similar behaviors are also misremembered. Is it true that when it comes to eating, "we get no help from our attention or our memory?"

Memory researchers have long recognized the adaptive benefits of forgetting (Anderson & Schooler, 2000; Bekinschtein, Weisstaub, Gallo, Renner, & Anderson, 2018; Kuhl, Dudukovic, Kahn, & Wagner, 2007). What's more, if the main goal of memory is to predict future events (Josselyn & Tonegawa, 2020; Mullally & Maguire, 2014; Schacter, Addis, & Buckner, 2007; Suddendorf & Corballis, 2007), there may be little need to be able to easily recall minute details of everyday experiences. Misra, Marconi, Peterson, & Kreiman (2018) provided a recent test of this. Participants wore a video-camera combined with an eye-tracker while walking several routes in Cambridge Massachusetts. The next day, participants completed an old/new recognition memory test where they were shown clips of their own walking experience or those of other participants. Participants were only slightly above chance in recognizing their own walking experiences compared to others, which suggests memory for the minor details of everyday events is poor. In light of this, it is reasonable to suspect that memory for eating should be

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no different than memory for any other behavior—which is, as it turns out, often poor and inaccurate due to the benefits of forgetting erroneous information.

Alternatively, it could be that memory for eating is more accurately remembered than other behaviors. That is, this underestimation bias that has worried some nutritional scientists may actually be fairly conservative relative to memory for other behaviors. There are three theoretical reasons to suggest this may be the case.

First, comparative studies in non-human animals suggest that episodic memory may have evolved in animals to benefit foraging. Birds such as Black-capped chickadees and Scrub Jays provide evidence as such as they, via enlargement and specialization of the hippocampus, can remember the exact location and even contents of food cached up to several months prior (Balda & Kamil, 1992; Clayton & Dickinson, 1998; Roberts et al., 2008; Sherry, Jacobs, & Gaulin, 1992). In rodents, episodic-like memory is shown as rats are tasked with remembering specific details about food, some of which has been devalued (Babb & Crystal, 2006; Roberts et al., 2008; Zhou & Crystal, 2009). These findings are suggestive of the idea that episodic memory evolved to benefit animals in foraging and obtaining food. Thus, memory of eating and for food relevant information may be particularly strong, as it reflects one of the main tasks the memory system was selected for.

Second, evolutionary influences on human memory are abundant. For more than a decade, researchers have observed preferential memory for fitness relevant stimuli or neutral stimuli processed in such a manner to make them fitness relevant. Nairne, Thompson, & Pandeirada (2007) provided the first demonstration of this, showing that neutral items processed on the basis of their relevance to an imagined survival scenario were better recalled than those exact same items processed based on their relevance to the non-evolutionarily important scenario of moving to a foreign land. A similar mnemonic benefit also exists for processing information based on its relevance to an imagined scenario involving the evolutionarily-important task of parenting/raising a child (Seitz, Polack, & Miller, 2018), as well as selecting a future mating partner (Pandeirada, Fernandes, Vasconcelos, & Nairne, 2017). Neutral items can be made more memorable if described as being touched by a sick individual compared to those same items touched by a healthy individual (Bonin, Thiebaut, Witt, & Méot, 2019; Fernandes, Pandeirada, Soares, & Nairne, 2017). Faces deemed to be trustworthy or untrustworthy are better remembered than neutral faces in an imagined survival scenario (Hou & Liu, 2019). Such findings demonstrate that the evolutionary significance of the information being encoded affects its ability to be subsequently recalled, which suggests the act of eating should be well remembered (Seitz, Blaisdell, Polack, & Miller, 2019). However, all of these studies rely on hypothetical or imagined scenarios. To truly understand the role of adaptation on selective memory, and to move the 'adaptive memory' literature forward, studies of actual behavior are needed. While it is well known that performing actions is better remembered than simply imagining them (Engelkamp, 1998), a functional perspective of memory predicts that actions more relevant to evolutionary fitness (e.g., eating) should be better recalled than actions less relevant to evolutionary fitness.

Third, memory of eating appears to play an important role in moderating future food consumption—which to do so, likely relies on enhanced memory of eating. Interfering with memory of eating, either through optogenetics in rats (Hannapel et al., 2019), or by distracting humans while they eat (Higgs & Woodward, 2009; Mittal, Stevenson, Oaten, & Miller, 2011; Oldham-Cooper, Hardman, Nicoll, Rogers, & Brunstrom, 2011), results in earlier onset of eating and increased amount of food consumed in the subsequent meal. By contrast, increasing memory of a meal, by instructing participants to focus on sensory aspects of the food and/or eating mindfully (Allirot et al., 2018; Higgs, 2015; Higgs & Donohoe, 2011; Robinson, Kersbergen, & Higgs, 2014; Seguias & Tapper, 2018) or cuing them to remember their last meal (Higgs, 2002; Szypula, Ahern, & Cheke, 2020), reduces total volume consumed during a following eating opportunity. Note that some manipulations aimed at enhancing attention during eating have not resulted in less subsequent snacking (Tapper & Seguias, 2020; Whitelock, Higgs, Brunstrom, Halford, & Robinson, 2018). If, however, memory of eating is already particularly strong—as we hypothesize—it may be the case that these enhancements in attention do not strengthen memory of eating significantly more than the control conditions (i.e., a ceiling effect). Thus, it may be easier to demonstrate that distracting participants during eating worsens memory of eating and leads to greater consumption rather than demonstrating that enhancements to memory of eating reduces future snacking. In any event, it is not unreasonable to suspect that given the important role that memory of eating plays in moderating future consumption, the act of eating may be particularly well remembered, either through enhancements in encoding, storage, or retrieval.

Thus, these three separate literatures inform the prediction that the act of eating should be well remembered. However, there is also reason to suspect memory of eating is no different than memory of any other behavior, or as some nutritional scientists might think, that memory of eating is surprisingly poor and inaccurate. In fact, some memory researchers might make the latter prediction, as the repetitive nature of eating three meals a day might make eating a particularly habitual behavior (White & McDonald, 2002) and one that is prone to much interference (Wixted, 2004). In this study, we created a novel task to test how memory of eating differs from memory of other similar procedural behaviors. Next, we investigated several factors that might influence memory of eating. As enhanced memory of eating is thought to reduce future food consumption, understanding what influences meal memories might help reduce overconsumption. The following experiments, therefore, represent early investigations into the strength and determinants of memory of eating.

Experiment 1

The objective of this experiment was to assess differences in memory for three similar behaviors—one that involved eating, another that involved handling food, and another that involved handling nonfood items. All participants completed what we henceforth refer to as the Memory of Eating Task (MEaT). The task is conceptually similar to that used by Morewedge, Huh, & Vosgerau (2010) who had participants imagine eating M&Ms or moving quarters before being assessed on hunger, except that in our task all participants actually performed an action and were then tested on their memory for that action. In brief, the task involves participants watching a video and cueing them to perform one of the three previously described behaviors every time a tone is sounded. While this task is not identical to a typical meal, it allows for systematic study of various components that might affect memory of eating and in this experiment allows us to compare memory of eating to memory of similar but non-eating behaviors. Further, while the tasks of eating versus moving M&Ms are similar in a number of ways, there are a number of differences (e.g., sensory complexity, amount of motor activity, auditory, taste, and olfactory feedback, etc.) between these tasks that could presumably influence memory (but see Experiment 3 for an attempt to control for all of these limitations).

Methods

Participants

A power analysis was utilized to detect a medium effect ($f = 0.25$) with 80% power (Faul, Erdfelder, Lang, & Buchner, 2007). A total of 159[1] participants (128 female) were recruited from the UCLA subject pool and were randomly assigned to each condition ($n = 53$). Body mass index (BMI) did not differ significantly between groups, $F(2, 156) = 1.05$, $p = 0.35$. All participants were asked to refrain from eating at least two hours before their study start time and those who reported having not done this were excluded from analysis.

Materials

Participants completed the experiment in individual rooms where they watched a video (a Malcom Gladwell TED Talk). Throughout the video, a 400 Hz tone was periodically presented for 1.0 s on the same random schedule for every subject, averaging 1 tone presentation per 30 s. Concurrent with the tone, the border surrounding the video flashed red for 1.0 s. Psychopy2 (Peirce et al., 2019) was used to create this program and the code and additional setup information for this experiment/task can be found here https://osf.io/ejtu6/.

Procedure

All sessions occurred between 10 am–12 pm and 3–5 pm. Participants were told a cover story that the objective of this study was to measure memory of verbal information while distracted, and that they would watch a video while completing a distracting task. The cover story served to prevent participants from focusing too much on their respective task. While participants watched a video, they were instructed to either eat M&Ms, move M&Ms from the bowl to the container, or move plastic beads from the bowl to the container every time a tone was sounded (*see* Fig. 1 *for a depiction of the setup)*. The two moving conditions were chosen to most closely mimic the behavior of eating (but note limitations above), and given the glass container's narrow neck, a distinct rattling noise was made each time an object was deposited into it, which served as a marking stimulus to make each event more salient (Lieberman & Thomas, 1986). The tone was presented over laptop speakers and the gray video frame turned red 30 times for all participants using the same random schedule. Thus, all participants performed their respective tasks exactly 30 times under identical environmental conditions, and this was confirmed by weighing the bowls after participants had left. After watching the video, participants were moved to a separate, isolated room, and were assessed on their memory for different elements of the film. The survey began with a brief distractor task consisting of 5 basic arithmetic questions. Participants then answered multiple choice questions about verbal information presented during the film (e.g., How many pounds of armor was Goliath wearing? The rock fired from David's sling had a stopping power roughly equal to what?). Participants were also asked to estimate the duration of the film and critically, how many times they performed their respective task. Finally, participants were asked to reconstruct their task context using a bank of 10 symbols. This involved recreating the arrangement of the 7 symbols that had been placed on the cardboard frame that had stood behind the video screen. After completing these questions, the participants' height and weight were measured and they were debriefed about the true nature of the study and compensated.

Fig. 1. Task setup. The bowl on the left was filled with either M&MS or beads. As the video played, a 400 Hz tone was randomly sounded and the background of the screen filled red. When this happened, participants either ate one M&M or moved one M&M or bead to the container on the right. This occurred 30 times and all participants were later asked on how many times they performed this task. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Measures

Following the eating event, the post-task survey included a number of questions with the aim at measuring episodic components of the event. Episodic memories contain specific personal information about an experienced event, such as what happened, and where it happened (Tulving, 1972). To assess the participants' episodic memory, we collected responses about "what" they ate, specifically how many items they consumed, and we also had participants recreate the task context. Memory for information presented during the video and the video's duration were included to (1) remain consistent with our cover story of measuring memory for verbal information while distracted and (2) serve as a baseline measure to compare group mnemonic performance. While we predict memory of eating to be more accurate for the eating condition relative to the moving conditions, it is also possible that the act of eating will strengthen contextual and episodic memories as well. These additional measures will allow us to evaluate this hypothesis.

Items Reported: The number of M&Ms (or beads) participants reported having eaten (or moved).

Task Error: The absolute value of 30 minus the number of items reported. Thus, this measure accounts for both underestimation and overestimation and is used to assess memory accuracy.

Temporal Memory Error: The absolute value of 15 minus the duration

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[1] In Experiment 1, a total of 180 participants were initially recruited to complete this experiment. In Experiment 2, 181 were recruited, in Experiment 3, 211 were recruited, and in Experiment 4, 84 were recruited. As we collected data, participants who did not meet our inclusion criteria were marked, and we continued collecting data until we reached our target N with only eligible participants. Participants were marked as ineligible from analysis if their post bowl weight was more than one standard deviation from their group mean (calculated after the first 53 participants per condition), or if they indicated having forgotten to eat (or move) an item, or if they indicated they had eaten (or moved) an item when they were not supposed to during the post task questionnaire. We also excluded all participants who indicated having eaten less than 2 h before participating. Analyses of our main hypotheses were only conducted once we reached our target N of 159 eligible participants—with the exception of Experiment 4 which ended early due to COVID-19.

reported. This accounts for underestimation and overestimation.

Contextual Memory Error: Error points were given for choosing the lure symbols or putting symbols in incorrect locations (max error = 10, min error = 0).

Verbal Memory Accuracy: The number of multiple-choice questions about the film that participants answered correctly (out of 5).

Results

Table 1 summarizes participant's memory accuracy for how many times they completed the task, their accuracy for recreating the task context, and their accuracy for information presented during the video and its duration. Fig. 2a summarizes the task memory error, which was the absolute value of the difference between the actual number of times the task was performed (30) and the reported number of times the task was performed for each of the three tasks. A one-way ANOVA revealed a main effect of tasks, $F(2, 156) = 5.77$, $p < 0.01$, $\eta^2 = 0.07$ with a Bayes factor of 8.31 in support of the alternative hypothesis. Planned comparisons showed that eating the M&Ms resulted in fewer errors than moving the M&Ms, $t(156) = 2.83$, $p = 0.005$, $d = 0.56$, or moving the beads, $t(156) = 3.05$, $p = 0.003$, $d = 0.59$. Thus, memory for eating was superior to the two highly similar but non-eating behaviors. To test contextual memory, participants were asked to reconstruct the task context given a bank of 10 symbols, and errors were counted for choosing the wrong symbol and/or placing the symbol in the wrong location (max error = 10). A one way ANOVA did not reveal a significant main effect of task, $F(2, 156) = 1.96$, $p = 0.14$, $\eta^2 = 0.03$, Bayes Factor in favor of the null (BF_{01}) = 3.0. Planned comparisons revealed that memory for the context was numerically, though not statistically, most accurate for the M&M eating condition than the M&M moving condition, $t(156) = 1.91$, $p = 0.06$, $d = 0.36$, $BF_{01} = 1.01$, or bead moving condition, $t(156) = 1.42$, $p = 0.16$, $d = 0.27$, $BF_{01} = 2.11$. There was no difference across tasks in memory for the verbal information from the video, which was assessed by 5 questions related to the video, $F(2, 156) < 1.0$, $BF_{01} = 12.74$, or memory for the duration of the video, $F(2, 156) < 1.0$, $BF_{01} = 10.64$. Thus, enhanced memory for the eating behavior was specific to the actual behavioral aspect of eating and did not affect other aspects of the event.

Experiment 2

The results from Experiment 1 suggest that some elements of memory of eating are more accurately recalled than memory for similar but noneating behaviors. Even handling M&Ms did not result in the same memory benefit as did consuming the M&Ms. This suggests that food handling is qualitatively different from food consumption. However, these data do not speak to the proximate mechanisms that result in this enhanced remembrance. It is also possible that the enhanced memory was not due to the behavior of eating *per se*, and was influenced by other factors. One plausible mechanism that could have enhanced memory is the energy provided by the glucose in the M&Ms. Pre and post task glucose consumption has been shown by others to increase task memory in humans (Glenn, Minor, Vervliet, & Craske, 2014) and rats (Winocur, 1995), albeit much larger quantities of glucose were used than what participants in our study consumed (Smith, Riby, Eekelen, & Foster, 2011). To test this alternative physiological mechanism behind the results in Experiment 1, we had all participants perform the task of bead moving, but some participants consumed as much glucose as those who ate the M&Ms in Experiment 1, while others consumed Stevia (a sweetener containing no glucose) or water. If human memory is biased towards remembering the act of eating, we should not observe memory difference among the three groups. Alternatively, if the energy hypothesis is correct, that is, that energy consumption is what drove the improved memory in the eating task, then only participants drinking glucose solution should show better memory in Experiment 2.

Table 1
Mean outcome measures and standard deviation (in parentheses) per condition from Experiment 1. Data come from a survey taken after completing the MEaT. All participants completed similar actions 30 times, the video lasted 15 min, the maximum context error score was 10, and the maximum verbal memory accuracy was 5.

	Eat M&M	Move M&M	Move Bead
Items Reported	22.49 (7.50)	17.83 (5.18)	17.60 (5.51)
Task Error	9.28 (5.08)	12.17 (5.18)	12.40 (5.51)
Temporal Memory Error	4.91 (4.28)	4.14 (3.84)	4.34 (4.50)
Context Error	5.45 (3.21)	6.49 (2.58)	6.23 (2.58)
Verbal Memory Accuracy	2.60 (1.26)	2.57 (1.15)	2.72 (0.91)

Methods

Participants

We recruited an additional 159 (Footnote 1) participants (119 female) based on the same power analysis for Experiment 1. There was no difference in BMI across conditions, $F(2, 156) = 2.22$, $p = 0.11$.

Materials

Most of the materials were the same as those used in Experiment 1 with the main exception that all participants were in the bead-moving condition, and the addition of solutions that subjects drank before and after the task. Fresh solutions were created every other day and were stored in a standard refrigerator at 40°F. Thirty M&Ms contain approximately 17 g of sugar; thus, we mixed a 1/2 cup of sugar (100 g of sugar) with 10 cups of water (~2366 g of water), which resulted in a ~4.0% sugar solution. An 8 oz (~9 g of sugar) cup was consumed both before and after the bead moving task, resulting in roughly 18 g of sugar consumed. The Stevia condition was created to determine the extent to which detecting sweet substances could affect memory performance in the absence of any glucose ingestion. We replaced the 1/2 cup of sugar with 12 g of Stevia (according to the conversion chart provided at https://sweetleaf.com/stevia-conversion-chart/), and 4 blind taste testers (undergraduate assistants) confirmed the two solutions to taste equally sweet (~4% sugar vs ~0.5% Stevia).

Procedure

All participants performed the same bead moving task as used in Experiment 1. Before and after completing the task, participants consumed a liquid solution. One group consumed a solution containing the same amount of glucose found in 30 M&Ms (~17 g of sugar), another drank water matched for sweetness using Stevia which is non-caloric and contains no glucose, and the third group simply drank water. The post task survey, procedure, and measures were identical to that used in Experiment 1.

Results

We measured the same dependent variables as in Experiment 1, which are summarized in Table 2. Recall performance for the bead moving task across the 3 groups is displayed in Fig. 2b. As predicted by the eating hypothesis, no differences in task error were found across groups, $F(2, 156) < 1.0$, $BF_{01} = 13.74$. There was also no difference in memory for the verbal information, $F(2, 156) < 1.0$, $BF_{01} = 13.77$, or the duration of the video, $F(2, 156) = 1.22$, $p = 0.30$, $BF_{01} = 5.63$. Unexpectedly, there was a significant effect of condition on memory for the task context, $F(2, 156) = 4.49$, $p = 0.013$, $\eta^2 = 0.07$, Bayes Factor of 2.84 in favor of the alternative, such that participants who drank water before and after performing the bead task better remembered the context compared to those who drank Sugar Water, $t(104) = 2.40$, $p = 0.05$, $d = 0.44$ and Stevia Water, $t(104) = 2.76$, $p = 0.02$, $d = 0.53$ (note: Tukey

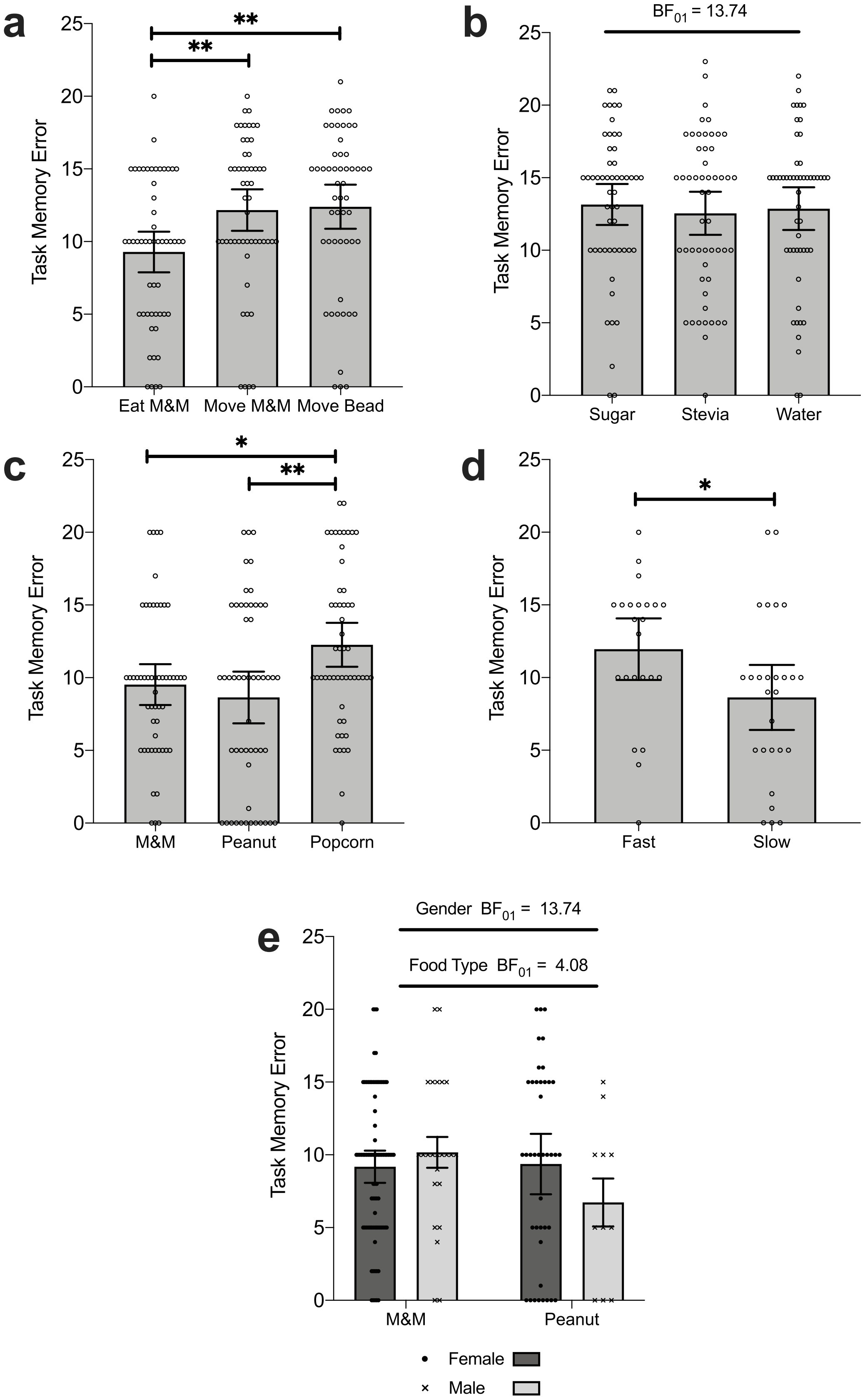

Fig. 2. (a) Memory accuracy for 3 similar procedural tasks performed under identical conditions. Error scores were calculated by taking the absolute value of the difference between 30 (actual number of times the task was performed) and the reported number of times the task was performed. Planned comparisons confirmed the eating task was best remembered. (b) Memory accuracy for the same bead moving task, but participants drank a liquid solution containing these additives before and after the task. No difference in memory performance despite glucose intake being equal for the Sugar and Eat M&M conditions. (c) Memory accuracy for eating 30 pieces of different food items. Participants who ate 30 of the calorically dense items (M&Ms or Peanuts) were more accurate in remembering how much they ate compared to those who ate 30 pieces of popcorn. (d) Memory accuracy for eating 30 M&Ms at a fast or slow eating rate. Slower eating was better remembered than fast eating. (e) Memory accuracy by gender and food type pooled across participants who ate M&Ms or peanuts in Experiments 1 and 3. There was no effect of gender or food type on recall. * = p value < .05, ** = p value < .01, *** = p value < .001, Error bars represent 95% confidence intervals. BF01 indicates Bayes Factor in support for the null.

Table 2

Mean outcome measures and standard deviation (in parentheses) per condition from Experiment 2. Data come from a survey taken after completing the MEaT. All participants moved a bead 30 times, the video lasted 15 min, the maximum context error score was 10, and the maximum verbal memory accuracy was 5.

	Sugar	Stevia	Water
Items Reported	17.3 (6.18)	17.45 (5.37)	17.25 (5.61)
Task Error	13.15 (5.13)	12.55 (5.37)	12.87 (5.34)
Temporal Memory Error	5.11 (4.09)	4.91 (5.23)	3.89 (3.48)
Context Error	6.81 (2.42)	6.98 (2.17)	5.68 (2.68)
Verbal Memory Accuracy	2.60 (1.12)	2.72 (1.04)	2.62 (1.04)

HSD post-hoc comparisons due to unplanned analysis). It is unclear why drinking the sweetened water attenuated memory of the task context relative to those who drank plain water. Nevertheless, the observed increase in memory performance for the M&M-eating group of Experiment 1 does not appear to be caused simply by the ingestion of glucose during the task, but instead suggests that the behavioral act of eating is better remembered than other similar procedural behaviors.

Experiment 3

Thus far, we have shown that memory of eating is particularly strong and that this effect does not appear to be driven by the glucose provided by the M&Ms in Experiment 1. Here we ask what factors influence memory of eating. Understanding the determinants of memory of eating is important because of the moderating role that these memories have on future food consumption. Evolutionary reasoning suggests caloric density may influence memory of eating because foods with more calories are of greater evolutionary value. New et al. (2007) provided indirect evidence of this. They had participants walk through a farmer's market and sample different food items. In a later test, memory for the location of the stand was linearly related to the caloric density of the food item being sold, such that the locations of more calorically dense food stands were better remembered. Others have also found enhanced spatial memory for calorically dense food items using a modified task in which participants needed to remember the location of various imaginary food items on a map (Allan & Allan, 2013; de Vries, de Vet, de Graaf, & Boesveldt, 2020). While all of these studies showed that caloric density may affect spatial memory of where the food was consumed, they were correlational in nature, and they do not speak to the effect of caloric density on memory for how much food was actually consumed. We sought direct evidence for whether or not memory differs for *consuming* the same number of food items that differ in their caloric density. This study, therefore, will provide the first evidence of how characteristics of the food item consumed affect memory of eating.

Participants

We recruited an additional 159 (Footnote 1) participants (117 female) based on the same power analysis for Experiment 1. There was no difference in BMI across conditions, $F(2,156) = 1.28$, $p = 0.28$.

Materials

All participants performed the MEaT as in Experiment 1, but we differed the food item consumed per condition. Bowls were filled to an equivalent level (3/4 of the bowl height) with the different items, which equated to 140 g of M&Ms, 90 g of salted peanuts, or 15 g of plain popcorn. These three items were selected due to that fact that they are similar in size and familiarity, because 30 of each item is not an unreasonable amount to consume per 15-minute session, and because we had previous success using M&Ms with this task. Additionally, while the popcorn is fairly flavorless and not calorically dense, the M&M and peanut are both flavorful and more densely caloric (around 5 calories per 1 piece) but differ on their specific taste (sweet versus salty) profile and sugar and fat contents. The popcorn was handmade and contained less than 1 calorie per piece (see Supplemental Material for additional nutritional information).

Procedure

The procedure was identical to that used in the M&M eating condition in Experiment 1. All participants consumed 30 of their respective food items on the same randomized schedule averaging to one item every 30 s. Our hypotheses and data analysis plan were pre-registered prior to data collection.

Results

We measured the same dependent variables as in the previous two experiments, see Table 3. Fig. 2c shows recall performance for eating the three different food items. As predicted, there was a significant effect of food item consumed on memory accuracy, $F(2,156) = 5.82$, $p < 0.01$, $\eta^2 = 0.07$ with a Bayes factor of 8.68 in support of the alternative hypothesis. Pre-registered planned comparisons revealed more accurate memory for eating the 30 M&Ms compared to the 30 pieces of popcorn, $t(156) = 2.47$, $p = 0.015$, $d = 0.52$, and for eating the 30 peanuts compared to the 30 pieces of popcorn, $t(156) = 3.27$, $p = 0.001$, $d = 0.61$. Similar to the findings from Experiment 1, there was no effect of food item consumed on memory for the duration of the film $F(2, 156) = 2.00$, $p = 0.14$, $BF_{01} = 2.89$, or verbal information presented during the film $F(2, 156) = 1.39$, $p = 0.25$, $BF_{01} = 4.90$. There was also no effect of food item on memory of the context, $F(2, 156) < 1.0$, $BF_{01} = 8.21$. Thus, the caloric density of the food item consumed appears to specifically influence the memory of how many times that food item was eaten, not other elements of the task. Finally, there was no difference in memory for eating the M&Ms from Experiment 1 and Experiment 3, $t(104) < 1.0$, $BF_{01} = 4.73$, which suggests the MEaT to be a reliable measure for studying memory of eating. At the same time, there was also no difference between the eat Popcorn condition and the move M&M condition from Experiment 1, $t(104) < 1.0$, $BF_{01} = 4.85$, which suggests memory of eating is not always superior to memory for noneating behaviors. Rather, and congruent with evolutionary reasoning, the human memory system appears to prioritize memory specifically for the consumption of high calorie or palatable foods.

Experiment 4

The results above suggest that memory of eating can be influenced by aspects of the consumed food item, specifically its caloric density. That said, holding the food item constant, there may be behavioral aspects of how food is consumed that affects memory for eating it. The rate of eating is likely to be one such factor, as distributed compared to massed encoding of information has long been known to facilitate retention (Underwood, 1961). Slower and more distributed eating should therefore result in better memory of eating than eating at a faster rate. Because memory of eating is thought to moderate future eating, better memory for slower eating might partially explain why a slower pace of

Table 3

Mean outcome measures and standard deviation (in parentheses) per condition from Experiment 3. Data come from a survey taken after completing the MEaT. All participants ate 30 of their respective food items, the video lasted 15 min, the maximum context error score was 10, and the maximum verbal memory accuracy was 5.

	M&Ms	Peanuts	Popcorn
Items Reported	21.83 (7.10)	22.30 (7.57)	20.00 (9.02)
Task Error	9.53 (5.09)	8.64 (6.45)	12.26 (5.47)
Temporal Memory Error	4.34 (4.80)	5.66 (6.48)	3.74 (3.45)
Context Error	6.38 (2.71)	6.30 (2.76)	6.89 (2.41)
Verbal Memory Accuracy	2.75 (0.96)	2.60 (1.13)	2.94 (1.06)

eating is associated with lower rates of obesity (Robinson, Almiron-Roig, et al., 2014).

To our knowledge, only two studies have to date examined how rate of eating influences memory of eating. Ferriday et al. (2015) controlled the rate of tomato soup delivery using a modified feeding tube. Participants who consumed the soup slowly were more accurate at remembering how much soup they had consumed three hours later. One limitation of this study is that consuming soup via a pump is a highly contrived eating scenario which may influence memory performance and have limited applicability to actual eating events. Additionally, having participants pour soup into a bowl based on their memory for how much they consumed is confounded by one's ability to accurately pour liquids into bowls. Because in the MEaT participants are picking up the food item and placing it in their mouths as opposed to food being pumped into their mouths, and the memory test simply involves recall of how many M&Ms were consumed, it provides a more ecologically valid test of how eating rate influences memory of eating.

Similar to the procedure used in the MEaT, Hawton et al., (2018) had participants consume a pasta dish either quickly (n = 11) or slowly (n = 10) and they controlled eating pace using an auditory cue. Two-hours later, participants who ate slowly were more accurate in recognizing the correct portion size of their pasta dish in an array of images. In addition to the small sample size, one potential limitation of this design, and that used by Ferriday et al., is that the memory test occurs several hours after consuming the food, and so responses may be influenced by participant hunger levels. That is, just as memory of eating influences subsequent hunger levels (Brunstrom et al., 2012), hunger levels might also influence reported memory of eating. In the MEaT, however, participants are asked to remember how much food they consumed just minutes after consuming it, which speaks more specifically to the strength of the encoded memory of eating before it may be influenced by other factors (e.g., hunger, retroactive interference, etc.). Therefore, in a pre-registered study, we used the MEaT to investigate the role of eating rate in immediate memory of eating.

Materials

All participants performed the MEaT as in Experiment 1 and 3, but the bowl was always filled with 140 g of M&Ms. The 15-minute video was changed to a 22.5 min video about the history of Los Angeles freeways.

Participants

We planned to recruit 128 participants to detect a medium sized effect (d = 0.5) with 88% power. However, after reaching 50 participants, our data collection was halted due to the COVID-19 pandemic. This number of participants affords 54% power to detect a medium (d = 0.5) effect and 87% power to detect a large effect (d = 0.8).

Procedure

In Experiments 1 and 3, participants were cued to eat on a random schedule that averaged out to one food item every 30 s. In this experiment, half of participants were assigned to a fast eating schedule (n = 23) that were cued to eat an M&M on average every 15 s, and half (n = 27) to a slow eating schedule that were cued to eat on average every 45 s. A longer video was chosen to allow participants in the slow condition to eat 30 M&Ms over the course of the entire video. Participants in the fast eating condition did not have their first tone presented until after 15 min of the video had passed. This was chosen so to equate the retention interval between both conditions. This should also protect against recency effects (i.e. better memory for the beginning of an event), hold the amount of time spent in the encoding environment and video content constant, and avoid having participants eat 30 M&Ms and then wait for a prolonged period of time. Following the eating task, all participants completed the same measures as in the previous experiments.

Results

Fig. 2d shows recall performance for eating 30 M&Ms at the two different eating rates. As predicted, and according to our pre-registered analysis plan, a one-tailed independent t test revealed memory for eating the 30 M&Ms to be more accurate for slow compared to fast eating, $t(48) = 2.21$, $p = 0.016$, $d = 0.63$, with a Bayes Factor of 3.86 in favor of the alternative hypothesis. However, there was no effect of eating rate on memory for the duration of the film $t(48) < 1.0$, $\mathrm{BF}_{01} = 2.68$, verbal information presented during the film, $t(48) < 1.0$, $\mathrm{BF}_{01} = 3.26$, or the task context, $t(48) < 1.0$, $\mathrm{BF}_{01} = 2.66$. These results suggest that a slower eating rate immediately increases memory of eating relative to a faster eating rate.

General discussion

We sought to evaluate the strength and determinants of memory of eating. While some nutritional scientists (e.g., Archer et al., 2018; Schoeller et al., 2013; Wansink, 2006) claim memory of eating to be unreliably poor and inaccurate it remains unclear if memory of eating differs from memory of other similar behaviors. On the contrary, given the evolutionary significance of eating and the role that memory of eating has on moderating future food consumption, it may be the case that the act of eating is relatively well-remembered. We created a novel behavioral task to assess this question and demonstrated that memory of eating is more accurately recalled than memory of similar but noneating behaviors. We then ruled out glucose as a potential confound of this effect and finally, we showed that the caloric density of a consumed food item and the rate at which it is eaten influences its ability to be remembered.

One possible explanation of our results in Experiments 1 and 3 is that they were driven primarily by the demographic characteristics of our participants. That is, given our recruiting participants via the UCLA psychology subject pool, our participants were predominantly women. Restrained eating, the tendency to limit daily food consumption, and various eating disorders are far more common among women than men (Johnson, Pratt, & Wardle, 2012; Mangweth-Matzek et al., 2014; Savage, Hoffman, & Birch, 2009). Thus, participants who ate M&Ms and/or peanuts in Experiments 1 and 3 might have better remembered that eating behavior not because of some inherently unique property of eating, but rather because of their concerns with the calories being consumed which would be salient to restrained women. This alternative account predicts that women should preferentially remember eating high calorie foods compared to men. We pooled all participants who ate either M&Ms (Exp 1 & 3) or peanuts (Exp 3) at the same eating rate and analyzed their recall data for the number of items consumed (see Fig. 2e). There was no effect of gender on task error, $F(1, 155) < 1.0$, $\mathrm{BF}_{01} = 4.65$, or of food type on task error $F(1, 155) = 2.95$, $p = 0.09$, $\mathrm{BF}_{01} = 4.08$, and a medium sized, but not statistically significant, interaction between gender and food type, $F(1, 155) = 3.54$, $p = 0.06$, $\eta^2 = 0.07$. The interaction was due to men better remembering peanuts (less task error). In Experiment 4, there was no effect of gender on task error, $F(1, 46) < 1.0$, or gender by eating rate interaction, $F(1, 46) < 1.0$ (see Table 4). In any event, it is clear that women did not significantly remember the act of eating high calorie foods better than men, which obviates the concern that participant gender explains our results.

One possible limitation of Experiment 3 is that we cannot be certain that it was the caloric density of the food items that drove differences in memory performance. That is, M&Ms, peanuts, and plain popcorn differ on a number of characteristics, not just caloric density. For example, they may vary on liking, familiarity, chewing effort, or palatability (but see '*Future Directions*' section for a potential solution). After running the first 15 participants, we decided to ask each participant how much they liked the food item they were given, as well as how often they consumed

Table 4
Mean outcome measures and standard deviation (in parentheses) per condition from Experiment 4. Data come from a survey taken after completing the MEaT. All participants ate 30 of their respective food items, the video lasted 22.5 min, the maximum context error score was 10, and the maximum verbal memory accuracy was 5.

	Fast	Slow
Items Reported	19.17 (7.13)	22.11 (6.68)
Task Error	11.96 (4.89)	8.63 (5.65)
Temporal Memory Error	5.67 (4.10)	4.80 (3.32)
Context Error	6.30 (3.42)	5.56 (2.97)
Verbal Memory Accuracy	3.39 (1.08)	3.52 (0.98)
Male Task Error	12.50 (4.89)	7.50 (5.56)
Female Task Error	11.77 (5.03)	9.29 (5.76)

that item using a 5-point Likert scale. An ANCOVA with task memory as the dependent variable, condition as the independent variable, and how much participants liked the food they were given as a covariate still yielded a significant effect of condition, $F(2, 140) = 4.94$, $p = 0.008$, $\eta^2 = 0.07$, and the covariate was not significant, $F(2, 140) < 1.0$. An ANCOVA with how often participants consumed the food item also yielded a significant effect of condition, $F(2, 140) = 5.73$, $p = 0.004$, $\eta^2 = 0.08$, and the covariate was not significant, $F(2, 140) = 1.83$, $p = 0.18$, $\eta^2 = 0.01$. All three items are crunchy, but peanuts and M&Ms require more effort to chew, so it is possible that effortful chewing influences meal memories. Higgs and Jones (2013) however, manipulated chewing effort by making some participants chew for 30 s per bite, and found no difference in memory for that meal, though prolonged chewers did eat less food at a subsequent snack. Finally, M&Ms and peanuts are more palatable than the plain popcorn, so it is possible that food palatability influences meal memories. Of course, for evolutionary reasons, foods high in calories tend to be perceived as palatable, and so it would be difficult to dissociate the two without using artificial substances. In fact, palatability could be an evolutionary proxy for a food's caloric value.

Throughout these experiments, we have been primarily concerned with memory accuracy—which can be contrasted with memory of quantity (Koriat & Goldsmith, 1996). All participants performed similar tasks the same number of times, and then we calculated the difference between participants' memory for how many times they performed the task and the actual number of times they performed the task (30 for participants in all conditions). One interesting finding was a heavy bias in underestimating the number of times participants completed their respective tasks. Of the 527 participants who completed the MEaT, only 21 reported having performed their respective action (eating or moving a food item or beads) more than 30 times, whereas 470 reported less than 30, and 36 reported exactly 30 (see Table 5). Note that we took several measures to ensure participants performed their respective tasks exactly 30 times (Footnote 1) and know of no theoretical reasons that would predict such drastic underestimation. Clearly, investigation into whether this underestimation bias exists for other procedural behaviors is warranted.

Table 5
Number of participants who reported performing their respective tasks less than, equal to, or greater than, 30 times. Note, all participants performed their respective tasks exactly 30 times.

Exp.	Condition	n	Reported < 30	Reported = 30	Reported > 30
1	Eat M&M	53	42	4	7
1	Move M&M	53	49	4	0
1	Move Bead	53	50	3	0
2	Sugar	53	49	2	2
2	Stevia	53	52	1	0
2	Water	53	50	2	1
3	M&Ms	53	46	3	4
3	Peanuts	53	39	12	2
3	Popcorn	53	49	1	3
4	Fast	23	21	1	1
4	Slow	27	23	3	1

Related to this discussion of memory accuracy is also that of memory of quantity and the prevalence of false memories (Koriat & Goldsmith, 1996). While we have shown memory of eating to be more accurately recalled than memory for similar non-eating behaviors, it remains unclear whether or not memory of eating is more or less susceptible to false memories than similar non-eating behaviors. The closest data we have related to this, is the number of "lure" symbols participants chose when recreating the task context. The number of lures chosen ranged from 0 to 3 but did not significantly differ between condition for any of the experiments (lowest p value > 0.072). Nevertheless, the MEaT could be modified to test this, by having participants eat or move a variety of different food items, and then asking participants to recall all of the different items that they ate/moved.

Finally, it is important to acknowledge that not all measures of memory were enhanced in the eating condition in Experiment 1, the peanut and M&M condition in Experiment 3, or the slow eating condition in Experiment 4 relative to the respective controls. Specifically, in all three of those experiments, it was only memory for the number of times the task was performed that was more accurately recalled (the "what" aspect of the event) and not memory for the task context (the "where" aspect). We can only speculate that from an evolutionary perspective, it would be advantageous for a foraging animal to remember the number of items or the amount of food that they consumed during an eating event. For example, there is important information gained by an animal remembering they consumed 20 ripe berries from a bush versus 2 ripe berries. Further, it is now clear that in both humans (Brunstrom et al., 2012; Higgs, 2002; Higgs & Spetter, 2018) and non-human animals (Hannapel et al., 2019), memory for the amount of food consumed at a recent meal moderates future hunger and eating—so it is not surprising this information is prioritized by our memory systems, at least immediately after eating.

It is surprising that memory for the task context was not enhanced by any of these tasks. In our bush with 20 versus 2 berries example above, one would imagine it is important both to remember the number of berries in the bush but also, and critically, where that bush is located. One explanation for our null effects was that our test of contextual memory was not sensitive enough to detect this effect, as it is true that in all conditions where task memory was enhanced contextual memory was also nominally, though not significantly, enhanced relative to the respective controls. Similarly, it could be that the cues surrounding the computer screen were not particularly informative in terms of signaling the location of food. Perhaps, if we had participants eat different meals in different rooms, each containing different contextual details, the details would become more relevant signals of location and therefore be connected more strongly to the eating event, and better remembered for higher calorie than lower calorie meals. That said, the few demonstrations that have more specifically examined memory for the location of various food items have shown that the caloric density of the food item does correlate with improved memory performance, such that the location of higher calorie food items are better remembered (Allan & Allan, 2013; de Vries et al., 2020; New, Krasnow, Truxaw, & Gaulin, 2007). Thus, we would encourage those who wish to use the MEaT to experimentally study memory of eating to explore different measures for assessing contextual memory.

Future directions

These four experiments represent early investigations into the strength of, and the factors that influence meal memories. That said, and as alluded to above, there is still much to learn. The procedure used in the studies reported here lends itself nicely to systematically studying the characteristics of food items that affect their memorability and we have made the materials necessary for the MEaT freely available (https://osf.io/ejtu6/). For instance, time of day, meal size, and eating with others are all factors that might contribute to memory of eating.

The MEaT, with some modifications, could be used to interrogate these potential influences. Additionally, whereas we performed the recall tests immediately after eating—to prevent potential interference and effects of hunger—one could delay the retention interval to several hours after eating. This may speak more closely to how memory of eating influences subsequent eating. Because eating involves input from all five senses, inexpensive knock-out procedures (e.g., a nose-clip, or blindfold) might be paired with the MEaT to determine sensory aspects that influence memory of eating. Further, the MEaT could be modified so as to explore differences in memory for olfactory cues—without having participants eat anything at all. For instance, are scents that reliably signal calories (e.g., freshly baked cookies) better remembered than scents that do signal fewer calories or none at all (e.g., rose water—c.f. de Vries et al., 2020)?

Whereas in Experiment 3 we report enhanced memory for high calorie foods, one could test the proximate mechanisms behind this effect by having all participants consume popcorn but some of which has been made more caloric with fat or sugar additives. Additionally, artificial sweeteners could be used to make some items (e.g., yogurt or brownies) sweet and calorically dense and others sweet but non-calorically dense. That said, if memory is simply tracking the sweetness of an item, that does not negate the evolutionary argument that memory has been shaped by selective pressures, as sweetness has historically been a highly reliable signal of, and therefore proxy for incoming calories (Seitz, Flaim, & Blaisdell, 2020). Finally, instead of using foods that can be easily itemized (e.g., M&Ms, peanuts, and popcorn), entire meals could be presented to participants who are then cued to take a "bite" with every presentation of the tone. While this approach suffers from the lack of standard "bite" size, it would increase the ecological validity of the task and could be used to study memory for the current task compared to semantic memory for one's average meal size. Along these lines, we could allow participants to eat as many food items as they think matches their prototypical meal, and then compare this remembered amount to some objective measure of average participant meal size.

We encourage these and other investigations because understanding the determinants of memory of eating could inform intervention strategies to enhance memory of eating in an effort to reduce overconsumption. This seems especially important given increased concerns over global overweight and obesity phenotypes. Even a small reduction in daily caloric consumption (e.g., 100 calories) is thought to prevent weight gain in most of the US population (Hill, Wyatt, Reed, & Peters, 2003). Extant studies that ask participants to mindfully eat (e.g., Seguias & Tapper, 2018) or that prime participants to remember their most recent meal before snacking (e.g., Higgs, 2002; Szypula et al., 2020) report reductions of snacking of about 50–130 calories, so it is possible that we can use these simple manipulations to enhance memory of eating to our advantage. In short, we feel the time is ripe for studying memory of eating.

Conclusion

The results reported here are, to our knowledge, the first demonstrations of superior memory for an evolutionarily-important task compared to an appropriately matched task with lesser fitness relevance, using an actual behavior rather than an imagined scenario. The results from Experiment 3, in particular, are the first to demonstrate differences in memory for eating the same number of different food items. This has important implications for the literature on "adaptive memory", which has primarily been studied using various imagined scenarios and how they affect recall of neutral words. While demonstrations such as the 'survival processing effect' are suggestive of evolutionary pressures on human memory, there are a number of proximate mechanisms (e.g., elaborative encoding) that some (e.g., Howe & Otgaar, 2013; Kroneisen, Erdfelder, & Buchner, 2013) suggest to underscore this theoretical position (but see Nairne & Pandeirada, 2016 for an important discussion of proximate versus ultimate explanations of this research). While there are certainly other proximate explanations that may explain our findings of enhanced memory of eating high calorie foods, those typically used to argue against the survival processing effect (elaborative processing, self-referential processing) likely do not apply. Demonstrating memory biases for real behaviors highlights the value of a functional approach to provide insights into human memory systems. As demonstrations of mnemonic biases towards fitness relevant information continue to mount (Seitz et al., 2019), they should be considered in revisions of memory models by replacing assumptions of equipotentiality of encoded information with evolutionarily-informed assumptions about *a priori* potentiation of information memorability based on perceived fitness relevance.

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Ethics statement

All studies were approved by the UCLA Institutional Review Board (IRB # 18-001447).

All participants provided consent before completing the study and were debriefed afterwards.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jml.2020.104192.

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