

The Context Repetition Effect: Predicted Events Are Remembered Better, Even When They Don't Happen

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A key function of the medial temporal lobe (MTL) is to generate predictions based on prior experience (Bar, 2009). We propose that these MTL-generated predictions guide learning, such that predictions from memory influence memory itself. Considering this proposal within a context-based theory of learning and memory leads to the unique hypothesis that the act of predicting an event from the current context can enhance later memory for that event, even if the event does not actually occur. We tested this hypothesis using a novel paradigm in which the contexts of some stimuli were repeated during an incidental learning task, without the stimuli themselves being repeated. Results from 4 experiments show clear behavioral evidence in support of this hypothesis: Participants were more likely to remember once-presented items if the temporal contexts of those items were later repeated. However, this effect only occurred in learning environments where predictions could be helpful.

Keywords: prediction, temporal context, recognition, memory, cognition

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The medial temporal lobe (MTL) memory system has traditionally been thought of as providing a way to remember the past, but a growing body of research points to the importance of the MTL for generating predictions about the future (e.g., Johnson, van der Meer, & Redish, 2007; Levy, 1989; Levy, Hocking, & Wu, 2005; for reviews, see Buckner, 2010; Lisman & Redish, 2009). The ability to predict the future based on past experiences is critical for at least two reasons. First, it affords utility in an evolutionary sense: A predictive memory system allows an organism to learn how to adapt its behavior in order to obtain rewards (e.g., food, shelter, sex, social status, and support) and avoid punishments (e.g., predators, poison, social rejection), thereby greatly enhancing the organism's chances for survival and reproductive success (Klein, Cosmides, Tooby, & Chance, 2002; Schacter, Addis, & Buckner, 2007). Second, a predictive memory system provides the information necessary for a wide array of neural and psychological processes, from simple stimulus–response learning (Rescorla & Wagner, 1972) to perception (e.g., Stokes, Atherton, Patai, & Nobre, 2012), emotion (Kirkland & Cunningham, 2011), and even complex social interactions (e.g., Mitchell, 2009). Indeed, the evidence for use of predictions from memory is so ubiquitous that Bar (2009) has proposed that prediction is a “universal principle in the operation of the human brain” (p. 1181).

If the use of predictions is a universal principle, as Bar (2009) suggests, then it stands to reason that not only should the memory

system generate predictions, it should also be influenced by those very predictions. That is, the act of predicting that an event will occur could influence memory for that event. This supposition raises a number of interesting questions, such as: How would such an effect manifest behaviorally? What are the cognitive processes that might give rise to such an effect? What are the brain circuits and neural processes through which memory might be influenced by predictions?

In this article, we address these questions within the framework of a theoretical model that integrates concepts from models of reinforcement learning into a well-established computational model of episodic memory. We start by briefly outlining the framework and showing that it makes the unique prediction of a *context repetition effect* (CRE): Repeating the context in which an event was previously experienced improves the subsequent memorability of the event, even when the event itself does not occur. We then describe a set of behavioral experiments in which we test this prediction and whether the CRE depends on predictability in the environment and the nature of the stimuli. Finally, we discuss the implications of our findings with regard to experimental design, theories of learning and memory, and the function of the MTL.

Temporal Context and Associative Learning

One of the core functions of the MTL memory system (hippocampus, perirhinal and parahippocampal cortices) is to associate stimuli to the context in which they are experienced (Davachi, 2006). Within the literature, context has been defined based on spatial location (e.g., Mizumori, Ragozzino, Cooper, & Leutgeb, 1999), environmental configuration (Fanselow, 2000), spatiotemporal relations (e.g., Hunsaker, Lee, & Kesner, 2008), sequence and relative time (e.g., Fortin, Agster, & Eichenbaum, 2002; Huppert & Piercy, 1976), and even internal goal states (Kennedy

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& Shapiro, 2004). Given this variety of definitions, it seems reasonable to view context broadly as a multidimensional feature space that comprises the distributed mental representations of all aspects of experience.

More narrowly, we can define temporal context as a recency-weighted running average of experience, including both the present externally driven and internally generated representations of the past (Howard & Kahana, 2002). Formal computational models that implement this definition have been shown to account for key data from studies of human memory (Polyn, Norman, & Kahana, 2009; Sederberg, Howard, & Kahana, 2008) as well as MTL function in animals (Howard, Fotedar, Datey, & Hasselmo, 2005). To aid the reader, we present a conceptual illustration of learning using temporal context below.

Imagine a school bus driver who is starting a new route and wants to learn the names of her passengers. For simplicity, assume that only one child gets on the bus at each stop. When the driver starts, her temporal context is simply the representation of an empty bus. At the first stop, Amy boards the bus. The driver binds a representation of Amy (the current state) to the current temporal context (empty bus). She then updates her temporal context to consist of Amy and a decayed representation of the empty bus. At the second stop, Burt gets on the bus. The driver now binds a representation of Burt to the temporal context (Amy and a decayed representation of the empty bus). Note that because the binding is between the current state and the temporal context, Burt is bound not only to Amy but also to the empty bus. The driver's temporal context now contains a representation of Burt, a decayed representation of Amy, and an even more decayed representation of the empty bus. At stop three, Charlie boards and gets bound to context, which then updates to include him. As the driver continues, she binds each additional child to the current temporal context, which continues to evolve.

In this example, the bus driver learns using a Hebbian learning rule that associates each child to the temporal context at the time that child boards the bus. Traditionally, models using a Hebbian rule learn simple pairwise associations between stimuli, such that Amy would be associated to Burt and Burt would be associated to Charlie, but Amy would not have any direct association to Charlie. However, because the temporal context contains representations of multiple recent events—albeit decayed representations—temporal context models learn more complex episodic associations, such that Amy is associated to Burt and to Charlie. Thus, if on the next day Amy boarded the bus, the driver could predict that Charlie would eventually board as well.

One of the major problems with Hebbian learning is that associative strengths can grow without bounds when stimuli are repeated (Goodhill & Barrow, 1994). This is particularly true for temporal context models that use a Hebbian learning rule, thereby limiting these models to situations in which there are no systematic repetitions of stimuli (Howard & Kahana, 2002). Recently, Shankar, Jagadisan, and Howard (2009) introduced a temporal context model that learns semantic (i.e., cortical) representations from large numbers of repetitions of items in different contexts by incorporating predictions into the semantic learning rule. Inspired in part by this semantic model, we have extended the family of episodic temporal context models by using an alternative prediction-based learning rule derived from studies of animal learning.

Prediction-Based Learning

A major problem in animal learning is explaining how organisms learn to optimally navigate environments to maximize rewards (Dayan & Balleine, 2002). The temporal difference successor representation (TD-SR; Dayan, 1993; White, 1995) provides an elegant solution to this reinforcement-learning problem by using the set of recently experienced states to predict possible future states. Although TD-SR and temporal context models were developed independently, TD-SR can be reformulated in terms of temporal context such that associations are learned between the temporal context and *both* the current state and predicted future states (for details, see Gershman, Moore, Todd, Norman, & Sederberg, 2012). In the special case when each stimulus is encountered only once, TD-SR reduces to the standard associative learning rule used by existing temporal context models of memory.

However, when stimuli are repeated, TD-SR and simple Hebbian learning diverge. Critically, Hebbian learning strengthens memory only for items that are actually repeated, whereas TD-SR strengthens memory both for items that are repeated and for items that are *predicted* to be repeated. Returning to our bus driver analogy, suppose on the second day of school the driver again picks up Amy and Burt at their stops. As she does so, she uses her previously learned associations to generate predictions about which children are coming next (e.g., Charlie). These predictions are then associated with the current temporal context. Thus, even if a new student, Donna, boards at the third stop instead of Charlie, memory for Charlie is strengthened via the prediction that he would be there.

In more formal terms, we can distinguish between learning rules that might be used in the brain by examining the behavioral effects of repetitions of temporal context. If the brain uses a simple Hebbian associative learning rule as used in most computational models of memory, then repeating the temporal context of a once-experienced event should have no effect on memory for that event. However, if the brain uses a TD-SR learning rule, then repeating the temporal context of a once-experienced event should increase associations in memory for that event relative to once-presented events whose temporal context is never repeated. Thus, memory for predicted events will be improved *even when the events themselves are not repeated*.

Overview of Experiments

We report a set of four experiments designed to test for the CRE in learning environments in which item repetitions either could be accurately predicted from context a proportion of the time (Experiments 1 and 2) or could never be predicted from context (Experiments 3 and 4). For each of these environments, we conducted identical experiments using pictures of indoor and outdoor scenes (Experiments 1 and 3) and medium- to high-frequency words (Experiments 2 and 4). Thus, the set of experiments comprised a 2 (Target Predictability: 50% vs. 0%) \times 2 (Stimuli: pictures vs. words) factorial design.

The Target Predictability factor tests whether the CRE depends on the how predictable repetitions are in the learning environment. Theoretically, prediction-based learning will only be useful if the predictions are reasonably accurate. Imagine a taxi driver who experiences the same context repeatedly (e.g., driving to the airport to pick up passengers) but with different events (passengers) each

time. If the driver were to use his previous experience to predict which passenger he will pick up next, his prediction would almost always be wrong. Ideally, the taxi driver's memory system should be adaptable enough to recognize this fact and ignore or discount predictions made in this unpredictable environment.

Given the ecological constraints of the utility of prediction, we assume that the brain modulates the use of predictions based on whether they provide useful information about the current environment (Grossberg, 1987). On the basis of this assumption, we hypothesized that the CRE will occur only when the learning environment actually contains target repetitions that can be predicted from context (Experiments 1 and 2, but not Experiments 3 and 4).

The Stimuli factor allowed us to test the generality of the CRE across stimuli with varying degrees of imageability and rehearsal. If the CRE is driven by an automatic (i.e., unconscious) memory encoding processes, then it should be invariant to these variables, and the CRE should be observed in both Experiments 1 and 2. However, if the memory CRE is driven by a more conscious memory mechanism, such as covert retrieval and rehearsal (Hasher & Zacks, 1979), or by a nonmemory process, such as visual perception, then it should be modulated by the stimulus characteristics.

Experiment 1: Images Seen in a Predictable Environment

Method

Participants. Participants were 40 undergraduate students at The Ohio State University. All participants in all experiments participated in exchange for partial course credit and provided informed consent in accordance with requirements of the local Institutional Review Board.

Design. A 2 (context: repeated vs. novel) \times 2 (targets: repeated vs. novel) within-subjects, within-list factorial design was used. Within each study list, the items were organized into triplets, with the first two items of each triplet setting the *context* for the triplet's third item (the *target*). The triplet organization existed solely for the analyses and was not made apparent to participants.

Figure 1 shows an example of the study list organization. All triplets were presented twice, with a random lag (six to 21 items) between the presentations. For triplets in the repeated context, repeated target (RCRT) condition, the same stimuli were presented in the same order on both presentations. In the repeated context, novel target (RCNT) triplets, the context items were the same on the second presentation as the first, but the target item was replaced with a new target. Together, these conditions ensured that whenever a context was repeated, there was a 50% chance that it would be followed by the original target, thereby establishing that predictions from context are useful at least part of the time.

The novel context conditions mirrored the repeated context conditions. In the novel context, repeated target (NCRT) triplets, the target item was repeated while the two context items were replaced with new items. In the novel context, novel target (NCNT) condition, all three items in the triplet were replaced on the second presentation.

Because the novel target conditions featured different targets for the first and second presentation of each triplet, they formed a set of four nested conditions—RCNT₁ and NCNT₁ for the first presentation of each triplet and RCNT₂ and NCNT₂ for the second presentation of the triplet—that are critical for testing whether a CRE occurs. Specifically, a CRE can be said to occur if memory is better for novel targets experienced in a context that is repeated (RCNT) than for novel targets experienced in a context that is not repeated (NCNT). Performing this contrast separately for targets from the first triplet presentation (RCNT₁ – NCNT₁) and targets from the second triplet presentation (RCNT₂ – NCNT₂) will help distinguish between associative and predictive accounts of the CRE.

Materials. Stimuli consisted of a pool of 645 color photographs of indoor (336) and outdoor (309) scenes used by Turk-Browne, Simon, and Sederberg (2012). For each participant, a total of 360 stimuli were drawn from the pool and randomly assigned to five study lists. Each study list consisted of four triplets in each experimental condition, for a total of 72 unique items and 96 item presentations. For each study list, a corresponding 96-item test list was constructed using the 20 targets plus 28 randomly selected context items and 48 lures randomly drawn from the stimulus pool. A custom program using the Python experiment programming library (Geller, Schleifer, Sederberg, Jacobs, & Kahana, 2007) was

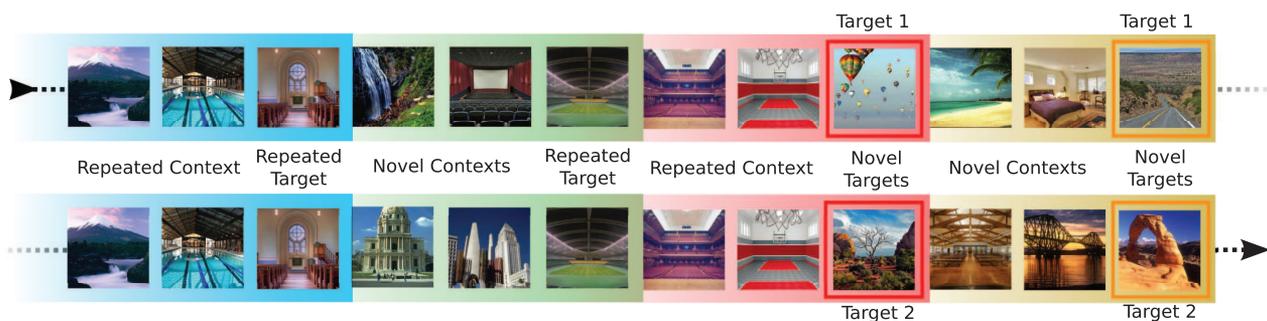


Figure 1. Example of a portion of a study list showing all four main conditions. From left to right: repeated context, repeated target, novel contexts, repeated target, repeated context, novel targets, and novel contexts, novel targets. The upper row shows the first presentation of the triplet in each condition, whereas the lower row shows the second presentation—appearing in the same order for demonstrative purposes.

used to generate the study and test lists for each participant, control the timing of the tasks, and record participant responses.

Procedure. Participants learned each of the five lists of stimuli, performed an *n*-back task for 5 min and were then given a surprise item-recognition test. During the learning phase, the stimuli were presented one at a time in the center of the screen for 1,200 ms each, with a 600- to 800-ms jittered interstimulus interval. For each stimulus, participants made an indoor/outdoor judgment by pressing one of two buttons on the keyboard. The surprise item-recognition test consisted of all target stimuli, a subset of the context stimuli, and an equal number of nonstudied lures, presented one at a time in random order. For each test item, participants indicated whether they thought it was “old” or “new” by pressing one of two buttons. Each test probe was displayed for 1,200 ms, with a 600- to 800-ms jittered interstimulus interval.

Results

Memory performance was measured as the mean proportion of tested items that were correctly identified as “old,” calculated separately for context items (the first two items in each triplet) and target items (the last item in each triplet) for each experimental condition (see Tables S1 and S2 in the supplemental material). A 2 (context repetition: novel vs. repeated) \times 2 (target repetition: novel vs. repeated) \times 2 (item type: context vs. target) repeated

measures analysis of variance (ANOVA) revealed main effects of context repetition, $F(1, 39) = 45.90$, $MSE = 0.0091$, $p < .0001$, and target repetition, $F(1, 39) = 12.15$, $MSE = 0.0119$, $p = .0012$, but no significant main effect of item type, $F(1, 39) = 2.08$, $MSE = 0.0080$, $p = .1570$. However, there were significant interactions with item type for both context repetition, $F(1, 39) = 26.36$, $MSE = 0.0084$, $p < .0001$, and target repetition, $F(1, 39) = 20.32$, $MSE = 0.0063$, $p < .0001$. Given the presence of these interactions, we next analyzed target and context items separately.

Memory for target items. A 2 (context repetition: novel vs. repeated) \times 2 (target repetition: novel vs. repeated) repeated measures ANOVA on target items revealed a main effect of target repetition, $F(1, 39) = 36.38$, $MSE = 0.0075$, $p < .0001$, with repeated targets ($M = 0.55$, $SEM = 0.017$) being remembered better than novel once-presented targets ($M = 0.47$, $SEM = 0.016$). There was no significant main effect of context repetition, $F(1, 39) = 1.75$, $MSE = 0.0087$, $p = .1940$, and no interaction between context and target repetition ($F < 1$). Thus, when examining memory for targets without regard to when the target was presented, the only effect was an item repetition effect.

However, a different story emerged when we examined the nested conditions for the presence of a context repetition effect. As can be seen in Figure 2, Panel A (see also Table S2 in the supplemental material), once-presented target items whose context

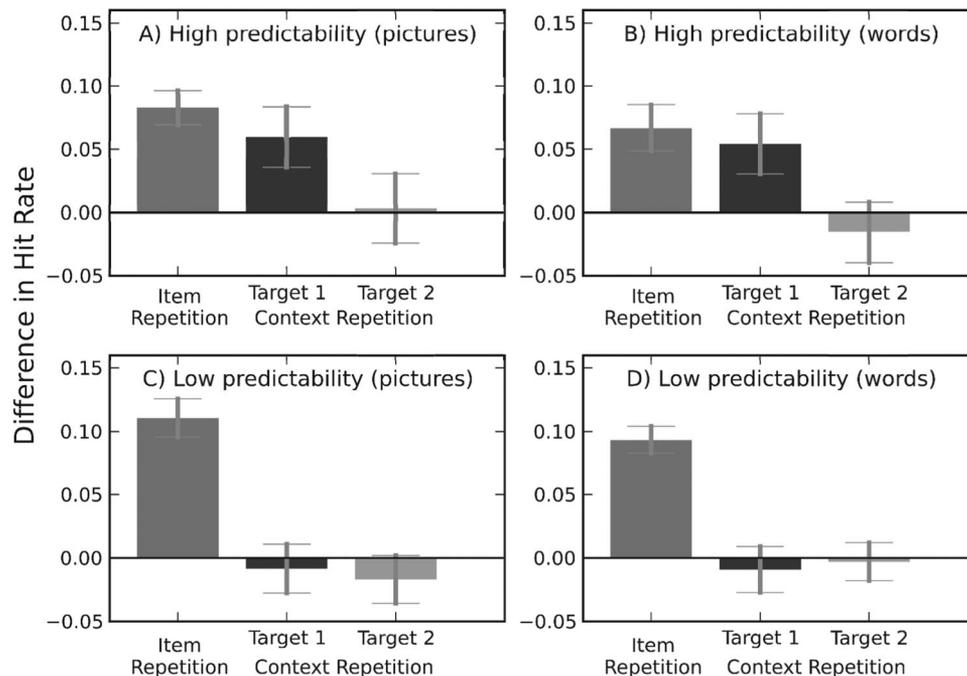


Figure 2. Item and context repetition effects for all experiments. A: Experiment 1: high degree of predictability when encoding pictures; B: Experiment 2: high degree of predictability when encoding word lists; C: Experiment 3: low degree of predictability when encoding pictures; D: Experiment 4: low degree of predictability when encoding word lists. Item repetition effect is the contrast between hit rates for all twice-presented targets (novel contexts, repeated target and repeated context, repeated target) versus Once-presented targets (novel contexts, novel targets [NCNT] and repeated context, novel targets [RCNT]). Context repetition effects are the contrasts between hit rates for once-presented targets preceded by a repeated context (RCNT) versus those preceded by a nonrepeated context (NCNT), calculated separately for the first and second targets associated to the repeated context and matched novel context. Error bars are standard errors of the mean calculated across participants.

was later repeated (RCNT₁) were remembered better than similarly once-presented targets that were preceded by a context that never repeated (NCNT₁), $t(39) = 2.46, p = .0185, \omega^2_{\text{partial}} = 0.06$. Just as importantly, there was no advantage for once-presented items with contexts that were already presented (RCNT₂) relative to corresponding once-presented items with novel contexts (NCNT₂), $t(39) = 0.11, p > .9$.

Memory for context items. A 2 (context repetition: novel vs. repeated) \times 2 (target repetition: novel vs. repeated) repeated measures ANOVA on context items revealed a main effect of context repetition, $F(1, 39) = 71.51, MSE = 0.0087, p < .0001$, with context items that were repeated ($M = 0.59, SEM = 0.018$) being remembered better than those that were presented only once ($M = 0.47, SEM = 0.015$). There was no significant main effect of target repetition and no interaction between context and target repetition ($F_s < 1$).

To test for a target repetition effect on context items analogous to the CRE on target items, we examined memory separately for the novel context items from the first and second triplet presentations in the repeated target (NCRT) and novel target (NCNT) conditions. Planned contrasts showed that later target repetition had no significant impact on memory for once-presented novel context items from the first presentation of the triplets, $t(39) = 0.1638, p > .80$, nor did target repetition impact memory for novel context items from the second triplet presentation, $t(39) = 0$.

Discussion

In Experiment 1, we tested whether memory for once-presented images within a moderately predictable environment would be influenced by the repetition of the context in which the image was originally experienced. Not surprisingly, we observed item repetition effects for both context and target images, with images that were presented twice being recognized better than items that were only presented once. We also observed a particular form of CRE. Repeating the context that had preceded a once-presented target image improved subsequent memory for that image but had no effect on memory for the new target image that followed the context repetition. Finally, there was no evidence for a bidirectional effect of repetition. That is, target repetition did not affect memory for context items.

This pattern of effects is counterintuitive and cannot be explained by traditional theories of memory. Theories that postulate that recognition is based purely on item strength (e.g., Murdock, 1993) would have no basis for predicting improved memorability for an item that was not re-presented. Theories that postulate that recognition is influenced by contextual associations (e.g., Dennis & Humphreys, 2001; Murdock, 1997; Shiffrin & Steyvers, 1997) might predict that repeating the context items increases the strength or quantity of the context memory traces, thereby making the targets associated to those context traces seem more familiar during test. This could explain the context repetition effect for the first targets in the repeated context conditions; however, such an account would also predict higher hit rates for the second targets, contrary to the pattern that we observed. Associative theories would also predict a target repetition effect in which repeating a target item enhances memory for the preceding context items, but there was no evidence for such an effect.

Our model parsimoniously explains the full pattern of results. The first time a context is experienced, the memory system has no knowledge about what should follow. Because predictions cannot be made, they can play no role in learning. When a context is later repeated, the target previously associated with it is predicted to be encountered next. This prediction reactivates the target and strengthens its association with the current context. Because the prediction occurs prior to the target event, the strengthening occurs regardless of whether the item is actually repeated, thereby generating the CRE. In the case in which the target repeats as predicted, the resulting prediction error is minimal, and little or no additional learning beyond the prediction-based boost occurs. This explains why the context prediction effect is nearly as strong as the item repetition effect. In the case when a nonpredicted novel target is presented, the second target is bound to the context with the same strength as other once-presented items that do not receive a prediction-encoding boost.

Experiment 2: Words Seen in a Predictable Environment

To verify that the results from Experiment 1 are replicable and not specific to stimuli that are highly visual (e.g., pictures), we ran an additional experiment using the identical design, but with words instead of pictures.

Method

Participants. Participants were 31 undergraduate students at The Ohio State University who participated in exchange for partial course credit.

Design, materials, and procedure. The design was identical to Experiment 1. For Experiment 2, the stimuli consisted of 630 medium- to high-frequency words selected from the University of Southern Florida free-association database (Nelson, McEvoy, & Schreiber, 2004). The procedure was also identical to Experiment 1 except that participants made living/nonliving judgments during the learning phase. The stimulus pool contained approximately the same number of items that were judged to be “living” and “non-living” in an internal pilot study.

Results

Mean hit rates for context and target items are shown in Tables S1 and S2, respectively, in the supplemental material. Similar to results from Experiment 1, a 2 (context repetition: novel vs. repeated) \times 2 (target repetition: novel vs. repeated) \times 2 (item type: context vs. target) repeated measures ANOVA revealed a significant main effect of context repetition, $F(1, 30) = 17.16, MSE = 0.0069, p = .0003$; a marginal main effect of target repetition, $F(1, 30) = 4.12, MSE = 0.0114, p = .0514$; but no significant main effect of item type ($F < 1$). There was also a significant Target Repetition \times Item Type interaction, $F(1, 30) = 8.79, MSE = 0.0123, p = .0059$, but unlike Experiment 1, the Context Repetition \times Item Type interaction was not statistically significant, $F(1, 30) = 1.31, MSE = 0.0112, p > .20$. Given the presence of an interaction, we next analyzed context and target items separately in analyses that parallel those used for Experiment 1.

Memory for target items. A 2 (context repetition: novel vs. repeated) \times 2 (target repetition: novel vs. repeated) repeated measures ANOVA on target items revealed a main effect of target repetition, $F(1, 30) = 13.09$, $MSE = 0.0115$, $p = .0011$, with repeated targets ($M = 0.67$, $SEM = 0.022$) being remembered better than novel once-presented targets ($M = 0.60$, $SEM = 0.018$). There was also a marginal main effect of context repetition, $F(1, 30) = 4.08$, $MSE = 0.0060$, $p = .0525$, with target items presented with repeated contexts ($M = 0.65$, $SEM = 0.022$) being remembered marginally better than target items presented with novel contexts ($M = 0.62$, $SEM = 0.019$). There was no evidence for a significant interaction between these factors ($F < 1$).

To test for a CRE, we performed planned contrasts on memory for novel target items between the repeated and novel context conditions. As can be seen in Figure 2, Panel B (see also Table S2 in the supplemental material), the critical results from Experiment 1 were replicated. A CRE was observed for target items from the first presentation of the triplets, $t(30) = 2.24$, $p = .0327$, $\omega_{\text{partial}}^2 = 0.06$, such that once-presented target items whose context was later repeated were remembered better than once-presented targets that were preceded by a context that did not repeat later. Also, there was no such effect for target items from the second presentation of the triplets, $t(30) = -0.63$, $p > .5$.

Memory for context items. Again replicating the results from Experiment 1, a 2 (context repetition: novel vs. repeated) \times 2 (target repetition: novel vs. repeated) repeated measures ANOVA on context items revealed a main effect of context repetition, $F(1, 30) = 8.94$, $MSE = 0.0120$, $p = .0055$, with context items that were repeated ($M = 0.67$, $SEM = 0.023$) being remembered better than those that were presented only once ($M = 0.61$, $SEM = 0.019$). There was no significant main effect of target repetition ($F < 1$), and no significant interaction between context and target repetition, $F(1, 30) = 2.95$, $MSE = 0.0138$, $p = .0964$.

Planned contrasts to test for a target repetition effect for novel targets analogous to the CRE showed that later target repetition had no significant impact on memory for once-presented context items from the first presentation of the triplets, $t(30) = 0.55$, $p > .50$, nor did target repetition impact memory for the novel context items from the second triplet presentation, $t(30) = 0.71$, $p > .40$.

Discussion

The main results from Experiment 1 were replicated in Experiment 2. We observed the expected item repetition effects for both context and target images as well as the CRE for novel targets whose context was later repeated. Again, there was no effect of context repetition on the second target item, nor was there any evidence for an effect of target repetition on memory for context items. These findings validate the results from Experiment 1 and show that the CRE is not specific to image stimuli.

Experiment 3: Images Seen in an Unpredictable Environment

In the study phase in Experiments 1 and 2, participants saw sequences of three items fully repeated at a later time (the RCRT condition) as well as sequences of two items repeated (the RCNT condition). These sequences may have served as a cue that the study lists contained predictable repetitions, thereby prompting the

encoding of predictions and the subsequent CRE. In Experiments 3 and 4, we remove the RCRT condition, thereby producing study lists where triplets are never repeated such that target item repetitions cannot be predicted from temporal context. If associations between predictions and temporal context are only learned when the current environment is perceived as predictable, this should eliminate the CRE.

Method

Participants. Participants were 52 undergraduates at The Ohio State University.

Design, materials, and procedure. The design of Experiment 3 differed from that of Experiment 1 in only one respect: To lower the predictability of the study lists, the RCRT condition was omitted, ensuring that participants never saw repeated sequences of more than two items. This modification led to a three-level within-subjects design featuring the NCRT, RCNT, and NCNT conditions, with both first and second presentations nested within the latter two conditions (RCNT₁, RCNT₂, NCNT₁, and NCNT₂). The materials and procedure were also identical to Experiment 1, with the following adjustments to accommodate the change in the design: For each participant, a total of 375 unique pictures were used, and participants viewed a total of 450 stimulus presentations, with 90 presentations in each of five blocks. Five test blocks were constructed, each featuring all 25 target items and 20 randomly chosen context items from the corresponding learning blocks, along with 45 lures.

Results

Mean hit rates for context and target items in each experimental condition are shown in Tables S1 and S2, respectively, in the supplemental material. Because the context and target repetition factors were not completely crossed as they were in Experiments 1 and 2, context and target repetition were flattened into a single factor for use in an omnibus 3 (condition: NCRT, RCNT, and NCNT) \times 2 (item type: context vs. target) repeated measures ANOVA. As expected, there was a significant main effect of condition, $F(2, 102) = 11.08$, $MSE = 0.0078$, $p < .0001$, and a significant interaction between condition and item type, $F(2, 102) = 42.49$, $MSE = 0.0072$, $p < .0001$. As in Experiments 1 and 2, there was no significant main effect of item type ($F < 1$). Planned pairwise t tests were used to identify the pattern of differences between the three experimental conditions separately for target items and context items.

Memory for target items. Consistent with Experiments 1 and 2, there was a robust item repetition effect for targets, but context repetition had no significant effect on overall memory for target items. Planned comparisons showed that memory was better for repeated targets than for novel targets, regardless of whether the preceding context items were novel, $t(51) = 6.45$, $p < .0001$, or repeated, $t(51) = 7.04$, $p < .0001$. There was no significant difference in overall memory for novel target items between the novel and repeated context conditions, $t(51) = 1.06$, $p > .20$.

To test for the CRE that was observed in Experiments 1 and 2, we separated out novel target items from the first and second triplet presentations. As Figure 2, Panel C (see also Table S2 in the supplemental material) shows, we found no evidence for a CRE for

once-presented novel targets from either the first triplet, $t(51) = -0.42$, $p > .60$, or the second triplet, $t(51) = -0.89$, $p > .30$, when the study lists had no target items that could be predicted from the preceding context items.

Memory for context items. Separate analyses of memory for the context items showed the same pattern of results observed in Experiments 1 and 2. There was a strong item repetition effect for context items, with repeated context items (RCNT) being remembered better than once-presented novel context items, regardless of whether the triplet contained a novel target item (NCNT), $t(51) = 4.81$, $p < .0001$, or a repeated target item (NCRT), $t(51) = 5.45$, $p < .0001$. There was no significant effect of target repetition on memory for context items, $t(51) = 0.22$, $p > .80$. We also examined target repetition effects for novel context items by triplet presentation and found no evidence for a target repetition effect on once-presented context items from either the first, $t(51) = 0.34$, $p > .70$, or second presentation, $t(51) = 0.03$, $p > .90$.

Discussion

Results from Experiment 3 were similar to those from Experiment 1, with the critical exception that there was no reliable CRE for target items. The fact that the only difference in the experiments was the removal of the RCRT condition from the design for Experiment 3 implies that this condition was necessary for the CRE. Of course, it is possible that the results from Experiment 3 are due to a Type II error; therefore, we ran an additional experiment without the RCRT condition, this time with words.

Experiment 4: Words Seen in an Unpredictable Environment

Method

Participants were 71 undergraduates at The Ohio State University. Experiment 4 replicated the design used in Experiment 3 but used the word-pool stimuli from Experiment 2 instead of images.

Results

Analyses for Experiment 4 paralleled those used for Experiment 3. An omnibus 3 (condition: NCRT, RCNT, and NCNT) \times 2 (item type: context vs. target) repeated measures ANOVA revealed a significant main effect of condition, $F(2, 140) = 16.63$, $MSE = 0.0065$, $p < .0001$, and a significant interaction between condition and item type, $F(2, 140) = 43.56$, $MSE = 0.0070$, $p < .0001$. As in the previous experiments, there was no significant main effect of item type ($F < 1$). This pattern of results is the same as was observed in Experiment 3.

Memory for target items. Further replicating the results from Experiment 3, there was a robust item repetition effect for targets, regardless of whether the preceding context items were novel, $t(70) = 7.24$, $p < .0001$, or repeated, $t(70) = 8.09$, $p < .0001$, and there was no significant difference in overall memory for novel target items between the novel and repeated context conditions, $t(70) = 0.53$, $p > .50$.

The critical test for the CRE required separated-out novel target items from the first and second triplet presentations. As Figure 2, Panel D (see also Table S2 in the supplemental material) shows,

we again found no evidence for a CRE for once-presented novel targets from either the first triplet, $t(70) = -0.50$, $p > .60$, or the second triplet, $t(51) = -0.19$, $p > .80$, when the study lists had no target items that could be predicted from the preceding context items.

Memory for context items. Separate analyses of memory for the context items also showed the same pattern of results observed in Experiment 3. There was a strong item repetition effect for context items, regardless of whether the novel context triplet contained a novel target item, $t(70) = 5.49$, $p < .0001$, or a repeated target item, $t(70) = 5.51$, $p < .0001$, and there was no significant effect of target repetition on memory for context items, $t(70) = 0.69$, $p > .40$. There was also no evidence for a target repetition effect on once-presented context items from either the first, $t(70) = 1.11$, $p > .20$, or second presentation, $t(70) = 0.05$, $p > .90$.

Discussion

The lack of a detectable CRE in Experiments 3 and 4 demonstrates an important boundary condition of the CRE: In a learning environment where meaningful predictions from context are not possible, a repetition of temporal context does not significantly enhance the memorability of events previously experienced in that context. Within the TD-SR framework, this finding implies that the learning system is sensitive to the utility of predictions and that it can modulate the influence that current predictions have on learning.

General Discussion

Neither the idea that context shapes memory nor the idea that prediction shapes memory is new; however, these ideas have only recently been linked to each other (e.g., Gershman et al., 2012; Nakahara, Itoh, Kawagoe, Takikawa, & Hikosaka, 2004; Turk-Browne et al., 2012). On the basis of a theoretical model in which memory encoding entails binding temporal context to both the current state and predicted future states, we hypothesized that memory for once-presented items can be improved by simply repeating their temporal contexts (i.e., without repeating the items themselves). This context repetition effect is a novel, counterintuitive prediction that has never before been reported. Across four experiments, we demonstrated the existence of the CRE along with a critical boundary condition for the effect: The CRE generalized across both picture and word stimuli but only occurred for lists that contained item repetitions that could be predicted from the temporal context. These findings demonstrate that prediction—and prediction alone—can enhance memory and that this only happens in an environment that is, at least partially, predictable.

How Common (and Important) Are Context Repetition Effects?

Our results and model imply that two critical conditions are necessary for the CRE. First, contexts must repeat when stimuli are being encoded into memory. Second, stimuli must repeat within the same context. Not every context or every stimulus need repeating, but the repetitions must occur often enough to establish that the environment contains predictable patterns of context and

item repetitions. These conditions explain why the effect has not been reported until now, challenge existing approaches to studying memory, and point toward future avenues of research.

In standard laboratory-based memory experiments with humans, repetitions of stimuli are generally avoided. The major exceptions to this rule are studies of item repetition effects (e.g., Ratcliff, Hockley, & McKoon, 1985) and studies of the spacing effect (e.g., Glenberg, 1979). However, even in these types of studies, presentation order is randomized or counterbalanced so as to avoid predictable patterns. Thus, unless the study is explicitly designed to examine the joint effects of repetitions of contexts and items, meeting the conditions necessary for the CRE is unlikely. Finally, we note that even if a study meets the necessary conditions, the CRE will only be detected if memory for the once-presented items whose context was repeated is contrasted with memory for items whose context was not repeated.

Importantly, the above-mentioned criteria not only explain why CREs are rare in laboratory research but also suggest that the phenomenon may be ubiquitous in natural memory. In the course of our everyday experiences, we generally encounter the same—or at least highly similar—temporal contexts repeatedly, often with the same types of events. For example, we may take the same bus to work each day at the same time of day, often seeing the same fellow passengers. Given the high degree of predictability in our everyday experience, prediction-based effects such as the CRE are likely much stronger and more common in the wild than would be expected based on the extant laboratory research.

By avoiding repetitions of context and items in their experiments, researchers have likely missed phenomena that are essential to understanding basic cognitive mechanisms. One solution to this problem is to augment laboratory research by taking advantage of technological advances and studying cognition in a more natural state (e.g., Milton et al., 2011). Another is to design experiments that acknowledge and try to mimic the repetitive nature of our everyday experiences.

An example of this latter approach is the work on reminding theory (Benjamin & Ross, 2011). In an innovative experiment, Tullis, Benjamin, and Ross (2012) had participants study word lists that contained semantically related words, matched unrelated words, and repetitions of words, all presented at spaced intervals. In a result that is similar to the CRE, memory for the first word in a pair was improved when the second word was a related word relative to when it was an unrelated word. Tullis et al. explained this effect as a consequence of reminding: When the second stimulus in a related pair is presented, it serves to remind the subject of the previous encounters with its semantic associate, and this reminding strengthens memory for the first word. Reminding thus serves as a high-level cognitive mechanism that is analogous to the low-level process of prediction-based learning.

Implications for Theories of Learning and Memory

The CRE challenges current theories of learning and memory because it implies that both context and prediction-based learning need to be incorporated into any viable theory. As we discuss below, the pattern of results from Experiments 1 and 2 cannot be explained by the standard associative binding mechanism that is at the heart of most theories of memory, including temporal context models (e.g., Howard & Kahana, 2002; Polyn et al., 2009; Seder-

berg et al., 2008), nor can they be explained by pure reinforcement learning models that use prediction error as a basis for learning (e.g., Dayan & Balleine, 2002). Instead, we propose that the CRE arises when the predictions themselves are the basis for learning.

Associative binding. One reason why prediction has not been a more important element in models of memory is that a great number of phenomena can be explained with a simple associative binding learning rule—especially when it is combined with competitive processes during retrieval (e.g., Raaijmakers & Shiffrin, 1981)—without invoking the need for prediction during learning. To illustrate why an associative binding model cannot account for the observed CRE, we revisit the example of the bus driver from the introduction.

As a reminder, the school bus driver is learning the names of the students on a new route. Assuming that she is using a learning rule that binds items to the temporal context in which they are experienced, after the third stop she would have a representation of Charlie that is bound to the context of Burt-Amy-bus. Similarly, each of the other students who board the bus as it continues on its route will be bound to a unique context, such that, on average, each of the student-to-context associations will be equal at the end of the day. Now, let us say that on the second day Amy and Burt board, just as on the first day, but then a new passenger, Donna, boards the bus instead of Charlie. Thus, Charlie is like an RCNT₁ item in our experiments, and Donna is like an RCNT₂ item.

If there is no prediction or retrieval during learning, both Charlie and Donna will now be associated to the Burt-Amy-bus context, and their associations to context will be the same as the strengths for other students who only rode the bus on Days 1 or 2, respectively. In the simplest model, in which associative strengths do not decay, Charlie and Donna would have the same strength of association to context and would therefore have the same probability of being remembered. If we allow associations to decay over time—whether due to interference, normalization, or some other process—Donna would have a larger associative strength than Charlie, and therefore a greater probability of being remembered later. However, in neither case would there be any difference in the strength of associations to context between Charlie and other students who only rode the bus on the first day (i.e., NCNT₁ items)—the critical comparison for the CRE we observed in Experiments 1 and 2.

But what if the model allows for retrievals during learning, such as hypothesized by Tullis et al. (2012)? On the second day, after Burt boards the bus, the driver could think back to the previous day and remember that Charlie had boarded next. This retrieval would then strengthen the association between context (Burt-Amy-bus) and Charlie, thereby increasing the memorability of Charlie relative to other students from the first day and thus producing a CRE. However, because associations are typically bidirectional, this process should also work in reverse. Imagine that on the second day, several new students board the bus before Charlie (so that Charlie is now a repeated target that follows a novel context). When Charlie boards, the driver would think back to the first day and remember that Burt and Amy boarded before Charlie, thereby increasing the memorability of Burt and Amy. In other words, a reminding account would predict that repetitions of targets should boost memory for context in the same way that repetitions of context boost memory for targets, but there was no evidence for such an effect in any of the experiments. Thus, an associative

account, even with retrieval during learning, does not seem to be able to explain how it is possible to obtain a CRE for the first target item but not the second.

Prediction-based learning versus prediction error. The fact that a CRE is observed for the first target item but not the second target item in the repeated context novel target conditions strongly implies that the mechanism driving the CRE has a temporal dependency. One way to ensure that there is a temporal dependency is to use a prediction-based learning rule in which predictions are made from the current context; context is updated with the event that actually occurred; and then the contextual associations for both the actual event and the predicted event are strengthened.

It should be noted that this process is different from the way in which prediction error is used in most unsupervised models of learning, including TD reinforcement learning. In these models, the prediction is compared with the outcome, and the difference (i.e., the prediction error) is used to modify memory. One of the consequences of this rule is that events that predicted but do not actually occur are unlearned. In simulations with a standard TD reinforcement learning model, we have observed that the context associations for the RCNT₁ item are initially boosted when the prediction is made following the repetition of the context items but then are almost immediately unlearned when a new novel target is presented and the prediction is not borne out. Thus, unlearning may be an advantage when predictions from memory are used to make decisions such as where to look for food because it helps an organism optimize the use of resources (Dayan & Niv, 2008); however, it may not be so desirable for an episodic memory system in which the goal is to remember both rewarded and unrewarded events.

Model-free and model-based learning. To be clear, we are not claiming that unsupervised learning does not occur in the brain or that our findings in any way challenge TD learning models, but we are claiming that TD learning models are not sufficient to explain all behavior—an idea that has been proposed even by advocates of TD models. For example, Daw, Niv, and Dayan (2005) proposed that the brain uses at least two distinct reinforcement learning systems to make behavioral choices—a model-free TD system that is associated with the dorsolateral striatum and is used for habitual control and a model-based system that is associated with prefrontal cortex-based decisions and is used for cognitive control. Both of these systems use memory to make predictions, but only the second requires an episodic memory that can be used to create mental models. Given the cognitive nature of the tasks in our experiments, the CRE would seem to be driven by this second system.

Environmental predictability. The fact that the CRE only occurs within predictable environments is also consistent with the dual-system framework proposed by Daw et al. (2005). In their model, the dorsolateral striatum and prefrontal systems generate uncertainty values on the basis of how well they are able to predict outcomes. These values feed a Bayesian arbitration process that determines which system to use to make a decision at any given time, thereby making the behavioral choice patterns dependent on the nature of the environment.

Although the predictability of events within the environment has generally not been considered within theories of memory, our results add weight to a series of recent studies showing that

environmental predictability is critical for a number of memory and cognitive processes. For example, prediction has been shown to be a key element that is necessary for the segmentation of events within episodic memory (for a review, see Zacks, Speer, Swallow, Braver, & Reynolds, 2007), and these predictability effects have been shown to be related to mechanisms within the prefrontal cortex and MTL (Ben-Yakov & Dudai, 2011; Ezzyat & Davachi, 2011). These same mechanisms have also been shown to be involved in generalizing memories across events (e.g., Shohamy & Wagner, 2008).

Context Repetition Effects in the Brain

In the introduction, we stated that our experiments were inspired by the idea that prediction is a universal principle in the brain (Bar, 2009). Although we have shown a clear behavioral effect, our current experiments did not address the broader question of how context and prediction are represented and used in the brain. This naturally raises a number of questions, many of which can only be answered by further experiments and theoretical development. We briefly outline two of the most important of these questions along with some potential answers.

The first and most obvious question is whether there is any evidence for CREs in the brain. Although no other studies have examined memory CREs, there is evidence for a perceptual CRE in studies of contextual effects on neural repetition attenuation (e.g., Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008; Turk-Browne et al., 2012). Summerfield et al. presented participants in a functional magnetic resonance imaging scanner with two faces separated by a short interstimulus interval. Faces were presented in contexts in which the second face was a repetition on either 25% or 75% of the trials. The typical reduction in the blood-oxygen-level-dependent (BOLD) signal in the fusiform gyrus was reduced when repetitions were improbable, suggesting that changes in neural repetition attenuation may reflect differences in prediction error. In a related study, Turk-Browne et al. (2012) had participants view streams of indoor/outdoor scenes that included both repetitions and nonrepetitions of context prior to a repetition of a target scene, similar to our RCNT and NCRT conditions. When an item repetition was preceded by a context repetition, the typical repetition attenuation of the BOLD signal in the parahippocampal cortex (PHC) was enhanced. This perceptual CRE is consistent with the idea that temporal context is used to predict repetitions, which then modulates activity in regions that code for the predicted stimulus, depending on the accuracy of the prediction.

The fact that the memory CRE replicated across words and scenes—two qualitatively different types of stimuli that are processed in different areas of the brain—raises the question of whether CREs might be observed in the brain in regions other than just the scene-selective areas of PHC examined by Summerfield et al. (2008) and Turk-Browne et al. (2012). Although neural repetition attenuation is most often found in visual ventral stream, studies have shown repetition attenuation effects in many other brain regions (for a review, see Henson, 2003). If the CRE is likewise found throughout the brain, it would bring an important new perspective to our understanding of perceptual processing and memory, greatly increasing the importance of context and prediction in determining how we represent our experiences. However,

finding that the CRE is limited to MTL regions—particularly those associated with visual perception or contextual memory—would further underscore the importance of the MTL in generating predictions for use by other brain regions.

Conclusion

Laboratory research on human cognition has largely ignored one of the major characteristics of natural environments—the repetition of predictable events. A few recent studies, including ours, recognize this fact and are finding novel, theory-driven effects of context-based predictions on behavior and neural processes. Effects such as the CRE are beginning to reveal the importance of prediction as a fundamental mechanism that may be at the center of cognition. Given that the predictive memory system likely evolved because it enhances the probability of obtaining rewards and avoiding punishments (Bar, 2009), perhaps we should not be surprised if it turns out that there is a close coupling between memory and reward, both in behavior and in the brain.

References

- Bar, M. (2009). Predictions: A universal principle in the operation of the human brain. *Philosophical Transactions of the Royal Society B, Biological Sciences*, 364, 1181–1182. doi:10.1098/rstb.2008.0321
- Benjamin, A. S., & Ross, B. H. (2011). The causes and consequences of reminding. In A. S. Benjamin (Ed.), *Successful remembering and successful forgetting: A Festschrift in honor of Robert A. Bjork* (pp. 71–87). New York, NY: Psychology Press.
- Ben-Yakov, A., & Dudai, Y. (2011). Constructing realistic engrams: Post-stimulus activity of hippocampus and dorsal striatum predicts subsequent episodic memory. *The Journal of Neuroscience*, 31, 9032–9042. doi:10.1523/JNEUROSCI.0702-11.2011
- Buckner, R. L. (2010). The role of the hippocampus in prediction and imagination. *Annual Review of Psychology*, 61, 27–48. doi:10.1146/annurev.psych.60.110707.163508
- Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology*, 16, 693–700. doi:10.1016/j.conb.2006.10.012
- Daw, N. D., Niv, Y., & Dayan, P. (2005). Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control. *Nature Neuroscience*, 8, 12, 1704–1711. doi:10.1038/nn1560
- Dayan, P. (1993). Improving generalization for temporal difference learning: The successor representation. *Neural Computation*, 5, 613–624. doi:10.1162/neco.1993.5.4.613
- Dayan, P., & Balleine, B. W. (2002). Reward, motivation, and reinforcement learning. *Neuron*, 36, 285–298. doi:10.1016/S0896-6273(02)00963-7
- Dayan, P., & Niv, Y. (2008). Reinforcement learning: The good, the bad and the ugly. *Current Opinion in Neurobiology*, 18, 185–196. doi:10.1016/j.conb.2008.08.003
- Dennis, S., & Humphreys, M. S. (2001). A context noise model of episodic word recognition. *Psychological Review*, 108, 452–478. doi:10.1037/0033-295X.108.2.452
- Ezzyat, Y., & Davachi, L. (2011). What constitutes an episode in episodic memory? *Psychological Science*, 22, 243–252. doi:10.1177/0956797610393742
- Fanselow, M. S. (2000). Contextual fear, gestalt memories, and the hippocampus. *Behavioural Brain Research*, 110, 73–81. doi:10.1016/S0166-4328(99)00186-2
- Fortin, N. J., Agster, K. L., & Eichenbaum, H. B. (2002). Critical role of the hippocampus in memory for sequences of events. *Nature Neuroscience*, 5, 458–462. doi:10.1038/nn834
- Geller, A. S., Schleifer, I. K., Sederberg, P. B., Jacobs, J., & Kahana, M. J. (2007). PyEPL: A cross-platform experiment-programming library. *Behavior Research Methods*, 39, 950–958. doi:10.3758/BF03192990
- Gershman, S. J., Moore, C. D., Todd, M. T., Norman, K. A., & Sederberg, P. B. (2012). The successor representation and temporal context. *Neural Computation*, 24, 1553–1568. doi:10.1162/NECO_a_00282
- Glenberg, A. M. (1979). Component-levels theory of the effects of spacing of repetitions on recall and recognition. *Memory & Cognition*, 7, 95–112. doi:10.3758/BF03197590
- Goodhill, G. J., & Barrow, H. G. (1994). The role of weight normalization in competitive learning. *Neural Computation*, 6, 255–269. doi:10.1162/neco.1994.6.2.255
- Grossberg, S. (1987). Competitive learning: From interactive activation to adaptive resonance. *Cognitive Science*, 11, 23–63. doi:10.1111/j.1551-6708.1987.tb00862.x
- Hasher, L., & Zacks, R. T. (1979). Automatic and effortful processes in memory. *Journal of Experimental Psychology: General*, 108, 356–388. doi:10.1037/0096-3445.108.3.356
- Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, 70, 53–81. doi:10.1016/S0301-0082(03)00086-8
- Howard, M. W., Fotedar, M. S., Datey, A. V., & Hasselmo, M. E. (2005). The temporal context model in spatial navigation and relational learning: Toward a common explanation of medial temporal lobe function across domains. *Psychological Review*, 112, 75–116. doi:10.1037/0033-295X.112.1.75
- Howard, M. W., & Kahana, M. J. (2002). A distributed representation of temporal context. *Journal of Mathematical Psychology*, 46, 3, 269–299. doi:10.1006/jmps.2001.1388
- Hunsaker, M. R., Lee, B., & Kesner, R. P. (2008). Evaluating the temporal context of episodic memory: The role of CA3 and CA1. *Behavioural Brain Research*, 188, 310–315. doi:10.1016/j.bbr.2007.11.015
- Huppert, F. A., & Piercy, M. (1976). Recognition memory in amnesic patients: Effect of temporal context and familiarity of material. *Cortex*, 12, 3–20.
- Johnson, A., van der Meer, M. A., & Redish, A. D. (2007). Integrating hippocampus and striatum in decision making. *Current Opinion in Neurobiology*, 17, 692–697. doi:10.1016/j.conb.2008.01.003
- Kennedy, P. J., & Shapiro, M. L. (2004). Retrieving memories via internal context requires the hippocampus. *The Journal of Neuroscience*, 24, 6979–6985. doi:10.1523/JNEUROSCI.1388-04.2004
- Kirkland, T., & Cunningham, W. A. (2011). Neural basis of affect and emotion. *WIREs Cognitive Science*, 2, 656–665. doi:10.1002/wcs.145
- Klein, S., Cosmides, L., Tooby, J., & Chance, S. (2002). Decisions and the evolution of memory: Multiple systems, multiple functions. *Psychological Review*, 109, 306–329. doi:10.1037/0033-295X.109.2.306
- Levy, W. B. (1989). A computational approach to hippocampal function. In R. D. Hawkins & G. H. Bower (Eds.), *Computational models of learning in simple neural systems* (pp. 243–305). New York, NY: Academic Press. doi:10.1016/S0079-7421(08)60113-9
- Levy, W. B., Hocking, A. B., & Wu, X. (2005). Interpreting hippocampal function as recording and forecasting. *Neural Networks*, 18, 1242–1264. doi:10.1016/j.neunet.2005.08.005
- Lisman, J., & Redish, A. D. (2009). Prediction, sequences and the hippocampus. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1193–1201. doi:10.1098/rstb.2008.0316
- Milton, F., Muhlert, N., Butler, C. R., Smith, A., Benattayallah, A., & Zeman, A. Z. (2011). An fMRI study of long-term everyday memory using SenseCam. *Memory*, 19, 733–744. doi:10.1080/09658211.2011.552185
- Mitchell, J. P. (2009). Inferences about mental states. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1309–1316. doi:10.1098/rstb.2008.0318
- Mizumori, S. J. Y., Ragozzino, K. E., Cooper, B. G., & Leutgeb, S. (1999). Hippocampal representational organization and spatial context. *Hip-*

- pocampus*, 9, 444–451. doi:10.1002/(SICI)1098-1063(1999)9:4<444::AID-HIPO10>3.0.CO;2-Z
- Murdock, B. B. (1993). TODAM2: A model for the storage and retrieval of item, associative, and serial-order information. *Psychological Review*, 100, 183–203. doi:10.1037/0033-295X.100.2.183
- Murdock, B. B. (1997). Context and mediators in a theory of distributed associative memory (TODAM2). *Psychological Review*, 104, 839–862. doi:10.1037/0033-295X.104.4.839
- Nakahara, H., Itoh, H., Kawagoe, R., Takikawa, Y., & Hikosaka, O. (2004). Dopamine neurons can represent context-dependent prediction error. *Neuron*, 41, 269–280. doi:10.1016/S0896-6273(03)00869-9
- Nelson, D. L., McEvoy, C. L., & Schreiber, T. A. (2004). The University of South Florida free association, rhyme, and word fragment norms. *Behavior Research Methods, Instruments, & Computers*, 36, 402–407. doi:10.3758/BF03195588
- Polyn, S. M., Norman, K. A., & Kahana, M. J. (2009). A context maintenance and retrieval model of organizational processes in free recall. *Psychological Review*, 116, 129–156. doi:10.1037/a0014420
- Raaijmakers, J. G., & Shiffrin, R. M. (1981). Search of associative memory. *Psychological Review*, 88, 93–134. doi:10.1037/0033-295X.88.2.93
- Ratcliff, R., Hockley, W., & McKoon, G. (1985). Components of activation: Repetition and priming effects in lexical decision and recognition. *Journal of Experimental Psychology: General*, 114, 435–450. doi:10.1037/0096-3445.114.4.435
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 64–99). New York, NY: Appleton-Century-Crofts.
- Schacter, D. L., Addis, D. R., & Buckner, R. L. (2007). Remembering the past to imagine the future: The prospective brain. *Nature Reviews Neuroscience*, 8, 657–661. doi:10.1038/nrn2213
- Sederberg, P. B., Howard, M. W., & Kahana, M. J. (2008). A context-based theory of recency and contiguity in free recall. *Psychological Review*, 115, 893–912. doi:10.1037/a0013396
- Shankar, K. H., Jagadisan, U. K. K., & Howard, M. W. (2009). Sequential learning using temporal context. *Journal of Mathematical Psychology*, 53, 474–485. doi:10.1016/j.jmp.2009.07.005
- Shiffrin, R. M., & Steyvers, M. (1997). A model for recognition memory: REM—retrieving effectively from memory. *Psychonomic Bulletin & Review*, 4, 145–166. doi:10.3758/BF03209391
- Shohamy, D., & Wagner, A. D. (2008). Integrating memories in the human brain: Hippocampal-midbrain encoding of overlapping events. *Neuron*, 60, 378–389. doi:10.1016/j.neuron.2008.09.023
- Stokes, M. G., Atherton, K., Patai, E. Z., & Nobre, A. C. (2012). Long-term memory prepares neural activity for perception. *Proceedings of the National Academy of Sciences*, 109, E360–E367. doi:10.1073/pnas.1108555108
- Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience*, 11, 1004–1006. doi:10.1038/nn.2163
- Tullis, J. G., Benjamin, A. S., & Ross, B. H. (2012). *The reminding effect: Presentation of associates enhances memory for related words in a list*. Unpublished manuscript.
- Turk-Browne, N. B., Simon, M. G., & Sederberg, P. B. (2012). Scene representations in parahippocampal cortex depend on temporal context. *Journal of Neuroscience*, 32, 7202–7207. doi:10.1523/JNEUROSCI.0942-12.2012
- White, L. (1995). *Temporal difference learning: Eligibility traces and the successor representation for actions*. Unpublished master's thesis, Department of Computer Science, University of Toronto.
- Zacks, J. M., Speer, N. K., Swallow, K. M., Braver, T. S., & Reynolds, J. R. (2007). Event perception: A mind-brain perspective. *Psychological Bulletin*, 133, 273–293. doi:10.1037/0033-2909.133.2.273

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