Building and breaking the chain: A model of reward prediction error integration and segmentation of memory

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Prediction errors drive reinforcement learning and organize episodic memory into distinct contexts, but do these effects interact? Here, we review the roles of midbrain dopamine, the locus coeruleus, and the hippocampus in event cognition to propose and simulate the theoretical influence of two prediction error signals in integrating versus segmenting events in memory. We suggest that signed reward prediction errors (SRPEs) can build mental models of reward environments, increasing the contextual similarity (integration) of experiences with stronger, more stable reward expectations. On the other hand, unsigned reward prediction errors (URPEs) can signal a new model of the environment, generating a contextual shift (segmentation) between experiences that crossed them. We moreover predicted that these differences in contextual similarity give rise to distinct patterns of temporal-order memory. We combined these ideas in a computational model to account for a seemingly paradoxical pattern of temporal-order memory where greater representational distance helps order memory within context but impairs it across contexts. We found that simulating SRPE integration and URPE segmentation differentially enabled the model to perform associative chaining, which involved reactivating items between two tested probes to assist with sequential retrieval. In sum, our simulations provide a unifying explanation for the varied ways that neuromodulatory systems may alter event cognition and memory.

Introduction

Structuring our experiences into distinct clusters helps us process and store vast amounts of information in memory. When needed, we can draw upon specific memories to guide how we think, feel, and behave in similar situations. A substantial body of work shows that predictability plays an important role in shaping this memory clustering process (Shin & DuBrow, 2021). For instance, prediction errors, which quantify the difference between our expectations and their outcomes, can act as signals that segment the stream of experience into separate memory representations (Bein et al., 2023; Zacks et al., 2007). In a reinforcement-learning framework, reward prediction errors (RPEs) also play a critical role in guiding how we learn to seek reward and avoid punishment (Rescorla & Wagner, 1972). Although episodic memory and reinforcement learning have been linked to distinct neural mechanisms (Eichenbaum & Cohen, 2004), recent work highlights the contribution of RPEs in orchestrating the interaction between these learning and memory systems (Antony et al., 2021; Rouhani et al., 2018, 2020; Rouhani, Niv, et al., 2023; Rouhani & Niv, 2021).

In this review and model simulation, we first discuss the roles of midbrain dopamine, the locus coeruleus (LC), and hippocampal memory processes to set the stage for a theoretical account of how signed reward prediction errors (SRPEs) at reward cue and unsigned reward prediction errors (URPEs) at reward outcome, structure events in episodic memory. We then simulate putative SRPE and URPE effects in a computational model of episodic memory that captures a previously unexplained pattern of temporal-order memory.

In our framework, we suggest that these two types of prediction error signals are mediated by the activation of separate arousal-related brainstem nuclei: the midbrain dopamine system and the locus coeruleus. We hypothesize that SRPEs elicited by cues that predict rewards, which are linked to increased dopamine release from the ventral tegmental area (VTA) (Schultz et al., 1997), promote the integration of rewarding experiences to build a mental model of the current, stable environment ('context'). Importantly, we focus on a building positive rather than negative SRPE (value) signal at reward cue (e.g., reward instead of loss expectation), associated with increasing (rather than decreasing) dopamine release (Kim et al., 2020; Schultz et al., 1997).

On the other hand, URPEs at reward outcome, quantifying the level of surprise, are linked to the LC (Sara, 2009), which co-releases dopamine and norepinephrine to influence hippocampal memory (Kempadoo et al., 2016; Takeuchi et al., 2016). It is theorized that spikes in LC activity indicate shifts in the underlying statistics of the environment, signaling the need for a new mental model (Bouret & Sara, 2005; Jordan, 2023; Sara & Bouret, 2012). Adapting to such shifts may lead to a perceived ‘event boundary’ between temporally-adjacent events, which parses experience into contextually-distinct representations in memory (Antony et al., 2021; Clewett et al., 2019, 2020; DuBrow et al., 2017; Rouhani et al., 2020; Shin & DuBrow, 2021).

Both VTA and LC neurons send projections to the hippocampus, suggesting they are well positioned to modulate mnemonic representations of time and context, including memory for the temporal order of events (Davachi & DuBrow, 2015; DuBrow et al., 2017; DuBrow & Davachi, 2016; Tubridy & Davachi, 2011). Order memory is thought to be guided by a contextual representation of events, which relies on hippocampal processes (Davachi & DuBrow, 2015). While several models of temporal-order memory have been proposed (Davachi & DuBrow, 2015; Friedman, 1993), we focus on associative chaining given behavioral (DuBrow & Davachi, 2013) and neural evidence (DuBrow & Davachi, 2014) for this mechanism. In associative chaining, when retrieving the order of two items, intervening items that had occurred between them are reinstated to help chain together their original sequence. In computational terms, items from the same context can better cue each other during retrieval through their contextual similarity (‘pattern similarity’), enabling the reconstruction of the original sequence. On the flip side, changes in context reduce the contextual overlap between items (‘pattern separation’), which prevents this cueing, and leads to impairments in temporal-order memory (DuBrow et al., 2017; DuBrow & Davachi, 2013, 2014, 2016).

We propose that SRPEs integrate across experiences to build reward expectation (i.e., generate expected values at reward cue) and maintain internal representations of contextual stability across time (pattern similarity in context), thereby enhancing memory for their temporal order. In contrast, URPEs that signal a shift into a new context drive the representation of the current context away from the previous one (pattern separation in context), impairing order memory between events that crossed them.

We tested our predictions in a variant of a computational model, the Context, Maintenance and Retrieval model (Horwath et al., 2023; Polyn et al., 2009; Rouhani et al., 2020). In the CMR, a slowly drifting internal context, whose degree of change is determined by the ‘contextual drift’ parameter of the model, creates temporal associations between the contexts of experienced items. We modified this network to include the theoretical effects of building

SRPEs at reward cues that slow down contextual drift to generate greater pattern similarity, or overlap, between the contexts of rewarding items. We also implemented model-update URPEs at reward outcomes to induce a sharp increase in contextual drift, generating greater pattern separation between the current and previous context. As changes in context have been characterized by both gradual 'drifts' and more sudden 'shifts' (DuBrow et al., 2017), in our model, large SRPEs slow contextual drift while large URPEs elicit contextual shifts.

Finally, we examined whether this modified network model could simulate a seemingly paradoxical pattern of temporal-order memory. Here, greater representational distance helps order memory for encountered items within a context yet impairs order memory for items across contexts (Pu et al., 2022; Rouhani et al., 2020). We implemented an associative chaining process during model recall to further examine whether the reactivation of intervening items between a tested pair predicted sequential retrieval (DuBrow & Davachi, 2013, 2014, 2016).

Building a stable model of the environment: The role of midbrain dopamine

Dopaminergic signals are widely recognized as an essential modulator of reinforcement learning systems. In foundational work, phasic, or transient, release of dopamine (DA) from the VTA has been shown to track the SRPE, increasing when outcomes are better than expected and decreasing when outcomes are worse than expected (Barto, 1995; Montague et al., 1996). With more learning, the presence of this phasic DA signal gradually shifts from outcome to the preceding cue that predicts reward, representing its value (Schultz et al., 1997). This DA signal was originally treated as a single, scalar 'model-free' value signal, driving behavior without the use of a model of the environment. Since then, it is now understood that DA transients may reflect multiplexed, 'model-based' value signals that build associations between stimuli to predict future rewards (Langdon et al., 2018; Sharpe, Batchelor, et al., 2017; Sharpe, Chang, et al., 2017). A new framework of mesolimbic DA further suggests that DA encodes causal associations between cues and their reward outcomes in memory (Jeong et al., 2022).

Phasic DA signals are therefore substantially implicated in constructing models of the environment, which enable reward predictions within a given context. In an unchanging learning environment, an accumulating SRPE signal integrates across past reward outcomes to generate stable reward values. Such increases in the stability of reward representations may enable memory mechanisms to prioritize the encoding of rewarding cues and their connections to related information (Jang et al., 2019; Rouhani & Niv, 2021; Stanek et al., 2019).

Building upon these models of midbrain DA function, we suggest that predictably rewarding cues may increase the temporal stability of the underlying context by decreasing the rate of contextual drift (Fig. 1B). Greater contextual similarity between items, in turn, may facilitate retrieval of those associated outcomes and the average value of that reward context, which is useful when encountering similar contexts in the future (Bornstein & Norman, 2017; Duszkiewicz et al., 2019).

Updating models of the environment: The role of the locus coeruleus

Tracking the stability of unfolding contexts is essential for binding multi-featured elements to a shared underlying memory representation. At the same time, packaging experiences into distinct events also requires balancing such integration processes with a memory separation process. Large URPEs representing a change in the underlying environment, help serve this purpose by prompting us to discard our current mental model in favor of a new one (Jordan, 2023). LC activity tracks URPEs (Sara, 2009) and is linked to enhanced attention and memory for concurrent information (Nieuwenhuis et al., 2005; Swallow & Jiang, 2010). While surprising outcomes may generally boost memory by heightening attention, the LC has been especially implicated in processing unexpected or inferred changes to the underlying model of the environment (Bouret & Sara, 2005; Jordan, 2023; Nassar et al., 2012; Sales et al., 2019; Yu & Dayan, 2005). During these model updates, LC releases norepinephrine (NE) to facilitate a 'network reset' across the brain, whereby functional brain networks are reconfigured to prioritize novel information and adjust behavior accordingly (Bouret and Sara, 2005; Sara, 2012). Pupil dilations, associated with phasic LC activity (Huang & Clewett, 2024; Joshi et al., 2016), moreover demonstrate selective sensitivity to these statistical or model-based violations (Antony et al., 2021; Kafkas, 2021; Zhao et al., 2019).

Such contextual change detection can segment events in memory, commonly indexed by worse memory for the temporal order of items that spanned a context shift, or event boundary, compared to items within a shared context (Clewett et al., 2020; Davachi & DuBrow, 2015; DuBrow & Davachi, 2013, 2014; Horner et al., 2016; Rouhani et al., 2020). Although attentional boosts can enhance memory encoding during arousing or large URPE outcomes, impairments in temporal-order memory are more reliably observed if there has been a change in the task or in the underlying reward distribution, which requires a model update (Rouhani et al., 2018, 2020; Rouhani, Niv, et al., 2023; Swallow et al., 2022; Wang & Egner, 2022, 2023). How the LC may support both memory enhancement and segmentation needs further clarification. Nonetheless, the effects of surprise versus a model update may be temporally dissociated: surprising outcomes predict an early increase in pupil dilation, whereas model-update outcomes predict a late decrease in pupil dilation (O'Reilly et al., 2013).

Here, we suggest that the LC supports model-update URPE outcomes by strengthening the activation of concurrent items in the underlying context at the expense of other active items (i.e., increasing the contextual drift). The enhancement of this model-update item at the expense of previous items, generates greater pattern separation between the current and prior context. Such separation, in turn, links experienced items to distinct underlying contexts in memory.

Memory remodeling at event boundaries: The role of the hippocampus

SRPEs from the midbrain and URPEs from the LC may both modulate dopamine-dependent plasticity in the hippocampus to predict episodic memory (Kempadoo et al., 2016; Lisman & Grace, 2005; Takeuchi et al., 2016). Hippocampal neurons moreover demonstrate gradually changing representations of a familiar environment (i.e., contextual drift), modulated by time (Bladon et al., 2019) as well as by experience (Geva et al., 2023; Khatib et al., 2023). In fMRI, greater hippocampal pattern similarity during item encoding moreover predicts stronger temporal-binding processes and order memory (DuBrow & Davachi, 2014). We propose that positive SRPEs during a reward cue, which gradually build accurate reward expectations in a stable learning environment, may slow down the rate of contextual drift. Reducing drift would increase pattern similarity between the contexts of items experienced in the same reward environment, which, in turn, increases the likelihood that items will episodically cue each other during retrieval.

The hippocampus also plays a role in discretizing experience into separate, non-interfering clusters (Clewett et al., 2019). When there has been a change in the underlying environment (e.g., an event boundary or model update), the hippocampus responds to its offset, reinstating the prior event to enhance the storage of recent details in memory (Baldassano et al., 2017; Ben-Yakov et al., 2013; Ben-Yakov & Dudai, 2011; Ben-Yakov & Henson, 2018; Lee &

Chen, 2022; Reagh et al., 2020; Silva et al., 2019; Sols et al., 2017). Activity in boundary-detecting neurons in the medial temporal lobe (including the hippocampus) has further been linked to stronger memory for items but worse temporal-order memory for boundary-spanning items (Zheng et al., 2022). These differential effects may be interpreted as a cognitive tradeoff, whereby encoding items is prioritized at the expense of binding inter-item associations across time (Heusser et al., 2018; Rouhani et al., 2020). Nevertheless, environments characterized by large URPEs (i.e., without changes to the underlying model) can demonstrate both enhanced item and temporal-order memory (Rouhani et al., 2018), pointing to a potentially selective effect of contextual shifts in segmenting memory.

Relatedly, the hippocampus is thought to maintain representations of contextual stability across meaningless fluctuations, such as sensory changes in the environment ((Dimsdale-Zucker et al., 2022; DuBrow et al., 2017; DuBrow & Davachi, 2016)). Rather than respond to any change in inputs, the hippocampus may specifically respond to boundaries that signal meaningful changes to the current model or task goals (Dimsdale-Zucker et al., 2022; DuBrow & Davachi, 2016). This observation further mirrors behavioral evidence that segmentation only occurs between items that require a new model of the environment (Rouhani, Niv, et al., 2023; Swallow et al., 2022; Wang & Egner, 2023).

Accordingly, we predict that model-update URPEs would generate a sharp increase in contextual drift, thereby separating the context of rewarding items into distinct underlying representations. Consequently, memories for items that occurred across the boundary event, including intervening items, are less likely to be reactivated at retrieval to assist with the reconstruction of sequential information.

Hippocampal subfields may moreover orchestrate event integration versus segmentation through different functional specializations. For example, the CA1 region, linked to novelty and prediction-error detection (Bein et al., 2020, 2023; Duncan et al., 2012), receives projections from midbrain dopamine as well as the locus coeruleus (Dahl et al., 2023). The dentate gyrus, on the other hand, associated with pattern separation of events in memory (Bakker et al., 2008), mostly receives projections from the locus coeruleus (Dahl et al., 2023), supporting the idea that LC-modulated URPEs promote pattern separation (Grella et al., 2021). We suggest that such pattern separation processes in the dentate gyrus may correspond with event segmentation effects in behavior.

The hippocampus also interacts with regions of the prefrontal cortex to support temporal encoding processes both within and across events (Clewett et al., 2019; DuBrow & Davachi, 2016). In fact, patients with frontal lobe lesions demonstrate selective impairments in temporal-order but not item memory (Shimamura et al., 1990). More specifically, model-update URPEs have been shown to segment representations in the medial prefrontal cortex (Antony et al., 2021) and orbitofrontal cortex (Nassar et al., 2019). These findings indicate that representations in the prefrontal cortex may be critical to supporting memory for the relative order of events, particularly after a period of memory consolidation (Tompary & Davachi, 2020).

Altogether, we propose a neuromechanistic model of event integration and segmentation based on the potentially distinct influence of different kinds of prediction errors on contextual memory. We suggest that SRPEs, relying on midbrain dopamine, increase at reward cues to build a predictable model of the environment. By contrast, we predict that large URPEs at reward outcome, linked to LC activation, indicate the need for a new model. These signals further interact with hippocampal processes that track and retrieve contextual and temporal representations from memory. In the next section, we simulate the potential influence of these RPE signals on a contextual representation of the environment to predict different patterns of temporal-order memory.

Figure 1. Theoretical and experimental paradigm. Reward prediction error signals and their neural substrates during a reward-conditioning task. In this task, participants learned to expect (and earn) rewards coupled with trial-unique scenes; large unsigned reward prediction errors (URPEs) indicated a change to the underlying reward distribution (a change in the mean of the received rewards, e.g., the scene with a 7¢ outcome; for experimental paradigm, see (Rouhani et al., 2020). During the cue that predicts reward (scene image presented prior to reward

outcome), theoretical signed reward prediction errors (SRPEs) are indicated in pink. SRPEs gradually build at the reward cue over the course of learning to represent the value of that experience. This signal is linked to phasic dopaminergic signals from the midbrain thought to influence hippocampal plasticity. To note, though SRPEs can also be negative (unlike URPEs), we include only the positive response at cue since the values in this task are all above 0, and a building negative RPE signal (conversely leading to a dip in phasic dopamine) is likely to produce distinct memory effects. URPEs at outcome, plotted in blue, are largest during the first trial (when participants do not know what to expect) and during subsequent 'model-update' outcomes when there has been a change in the mean of the underlying reward distribution. Large URPEs have been associated with dopaminergic and noradrenergic signals from the locus coeruleus which modulate hippocampal memory.

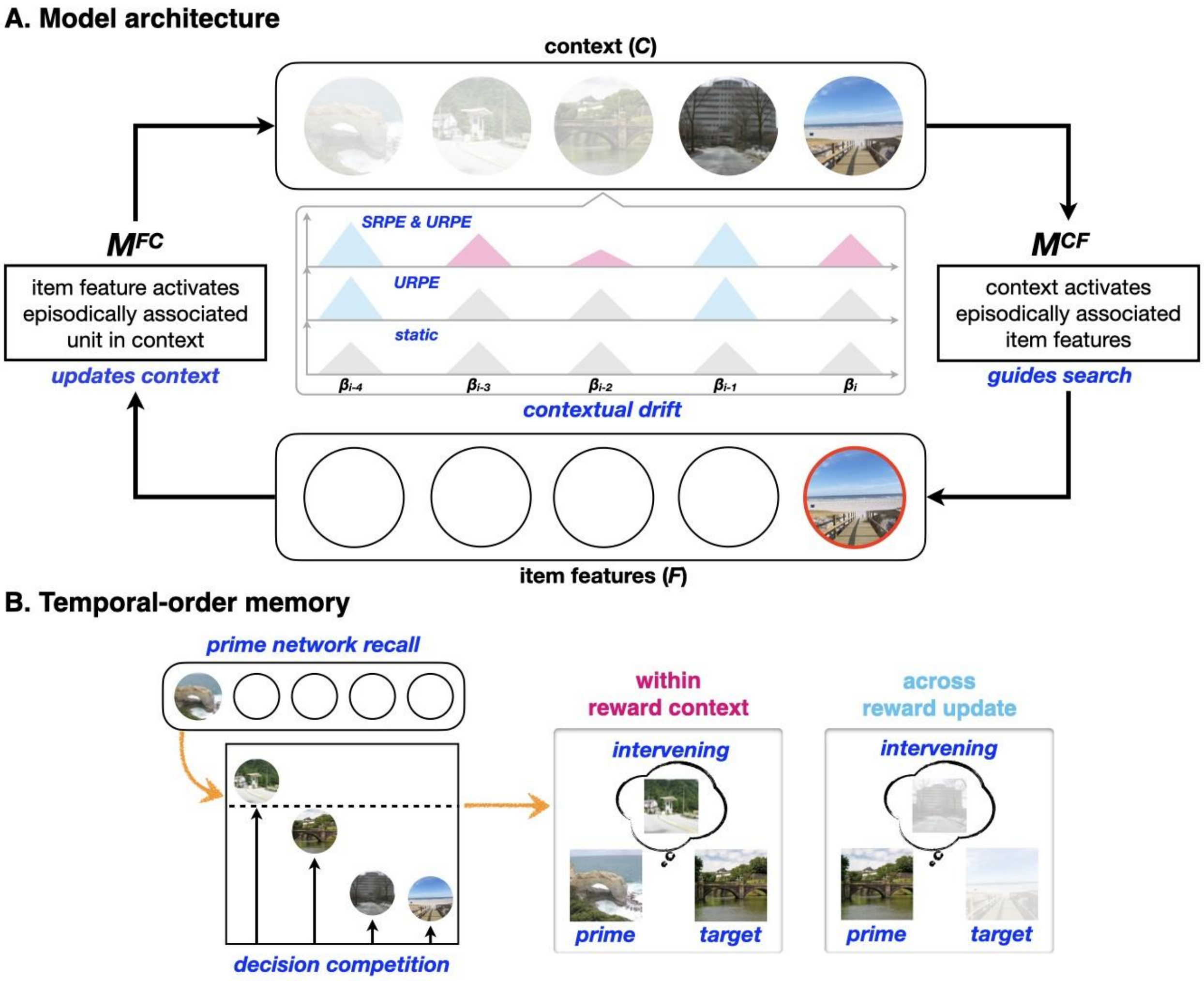
Computational model

Experimental task

We aimed to test our theoretical predictions by simulating behavior from a study which showed that model-update URPEs create event boundaries in memory (Rouhani et al., 2020). During encoding, participants completed a reward-conditioning task where they observed a sequence of trial-unique scene stimuli along with reward outcomes (a proportion of which they received, Fig. 1). The reward amount on each trial was contingent on the average value of the reward context, which would shift after 5-9 trials in every block (4-5 shifts per block). In Experiment 4 (and its replication), after this encoding phase, participants were asked to order two scene items by indicating which came first. The tested scene pairs were either encountered within or across reward contexts and had been 0, 1 or 3 trials apart during encoding. Order memory was impaired for items that crossed the model-update item, which indicated the start of a new reward context (1 or 3 trials apart; mixed-effects logistic regression: $B = -0.20$, $z = -4.79$, $p < 0.001$; Fig 3A). Moreover, order memory improved for more distant item pairs that were encountered in the same reward context ($B = 0.14$, $z = 2.60$, $p = 0.009$; Fig 3A) but not for item pairs that crossed contexts ($B = 0.11$, $z = 1.47$, $p = 0.14$; Fig 3A).

We hypothesized that as participants came to expect the reward outcome at cue, quantified by increasing SRPEs (Fig. 1 in pink), the contextual drift would decrease, leading to greater similarity between the rewarding items' contexts. On the other hand, when large URPEs at reward outcome signaled the beginning of a new reward context (model-update item, Fig. 1 in blue), we expected contextual drift to sharply increase, thereby separating the contexts of rewarding items by the underlying mean of the reward distribution. In these instances, the SRPE contextual drift subsequently resets, reflecting learning of a new reward context. Notably, while each trial during reward conditioning was associated with an SRPE and URPE signal at different timepoints (cue versus outcome), our model implements a single contextual drift for each trial. The trial- (or item-) specific contextual drift is governed by the SRPE within a reward context and the URPE during a model-update outcome that initiates a new reward context (for a visualization, see Fig. 2A, 'SRPE & URPE contextual drift').

In the experimental task (Fig. 1), the SRPE at reward cue and URPE at reward outcome were moreover associated with the same scene (the scene was initially presented alone, followed by its reward outcome; (Rouhani et al., 2020). The scene that would come to be associated with a model-update outcome therefore shared a context (and a high SRPE) with the preceding item during its cue phase (before outcome presentation), potentially explaining why an event boundary was not detected between the model-update scene and its direct predecessor. In our simulation, we therefore focused on pairs that were unambiguously across the event boundary in this task (pairs that had been 1 and 3 trials apart during encoding).


A. Model architecture

B. Temporal-order memory

Figure 2. A. Computational model simulating the effects of reward prediction errors on order memory. To test the mechanism supporting the effects of reward prediction errors on order memory, we used a variant of the Context, Maintenance and Retrieval model (Horwath et al., 2023; Polyn et al., 2009; Rouhani et al., 2020). In this model, experienced items first activate their corresponding unit in the feature layer (*F*, 'item features'), then this activation spreads upward to update the context layer (*C*) via the feature-to-context associative matrix (M^{FC}). The contextual drift parameter determines the extent to which a new item activates its corresponding unit in *C*, crowding out the activation of previously encoded items. The sequence in *C* reflects this diminishing activation of items given their order of presentation. During retrieval, activation in *C* spreads down to *F* via the context-to-feature associative matrix (M^{CF}), wherein features that had been episodically linked to the present state of *C* are activated and compete for retrieval (see 'decision competition' in panel B). We also simulated different sequences of contextual drift given the theoretical contribution of unsigned reward prediction errors (URPEs, in blue) and signed reward prediction errors (SRPEs, in pink) in modulating *C* during encoding (note that in the actual stimulation, 8 items, instead of the pictured 3, constituted a reward context). We propose a CMR model ('SRPE & URPE contextual drift') in which increasing SRPEs at reward cue decrease the contextual drift in a stable reward context, whereas large URPEs (indicating a model-update process) generate sharp increases in contextual drift. The latter effect results in the creation of separate reward contexts in memory (e.g., the stronger difference in activation between the third and fourth presented scenes in *C*). We compared episodic recall of this model to one that only included the URPE drift ('URPE contextual drift') and one that excluded both RPE modulators (i.e., a static drift parameter). **B. Temporal-order memory.** After encoding, we simulated temporal-order memory (judging which of two items occurred first or second) by priming the network with each item in a tested pair ('prime'). We then tallied the number of successful episodic retrievals of the other item in the pair ('target') during the decision competition. We further examined an associative chaining account of temporal-order memory by testing whether network reactivation of intervening items (i.e., those items encountered between the prime and the target) predicted the successful retrieval of the target item. We examined whether greater contextual similarity for items experienced within the same reward context increased the likelihood that intervening items were reactivated ('within-reward context') compared to those across a model-update ('across-reward update'). Additionally, within the same reward context, we predicted that item pairs that were separated by more trials at encoding (3-trials versus 1-trial apart) would further bolster intervening-item reactivation to successfully retrieve the target item.

Model overview

We tested a mechanism that guides the extent of pattern similarity (or separation) in the contexts of rewarding items to predict both improving temporal memory for more distant items within the same reward context as well as its disruption across a reward-context (or 'model') update. We implemented a variant of the CMR (Polyn et al., 2009) developed to examine the mechanism supporting event segmentation for large URPEs (Rouhani et al., 2020). In this computational model, each experienced item activates its corresponding unit in a drifting internal representation of the context, represented by a vector of previously experienced items ('context vector') whose activations decrease with time; the extent of this decrease is governed by the contextual drift parameter (Fig. 2A). A sequence of experienced items are thus temporally linked to each other through co-active units in context. Large (model-update) URPE items break the contextual association between items by updating context with higher activation, crowding out previously active items (i.e., causing the context to drift more).

We previously simulated temporal-order memory by relying on distance theories of temporal judgment (Friedman, 1993, 2004), which predicted behavior that was opposite to our results (Rouhani et al., 2020). In distance theories, greater dissimilarity between the context at encoding and test would predict that a more distant (i.e., pattern separated) item, such as one occurring prior to a model update, would be accurately judged as having occurred earlier than one that occurred after it (Hintzman, 2002). We instead found reliable impairment in temporal-order memory for pairs that crossed large URPEs despite the contextual distance between those items (Rouhani et al., 2020). Nonetheless, recent computational modeling work offers a process relying on distance theories that aims to explain this pattern of behavior (Pu et al., 2022). In this model, event boundaries reset the initial encoding context. During retrieval, the distance between the contextual representations of the probed items are compared to the initial encoding context. Items that occur after a boundary, and are therefore more similar to this reference point, are inaccurately judged as less recent. This mechanism relies on the assumption that a proportion of the initial encoding context continues to be reinstated at every event boundary and that this initial context is used as a reference point when making order judgments.

In the following simulation, we instead examined an associative chaining model of order memory (Caplan et al., 2022; Friedman, 1993). In the chaining model, intervening items between a tested pair of items are reactivated to facilitate order judgments. The mnemonic cueing of items through context makes reactivation more likely for intervening items that had shared a context versus those that had crossed a boundary during encoding (DuBrow & Davachi, 2013, 2014, 2016). To this end, we examined both retrieval success of the corresponding (‘target’) item in a tested pair as well as the number of intervening items that were reactivated (i.e., retrieved in the model) prior to recalling the target item. To explain how order memory discriminations improve for more distant items within the same reward context, we further manipulated the drift parameter of the original URPE model (Rouhani et al., 2020). In this simulation, not only does the drift increase at model-update URPEs, but also decreases trial-by-trial for items within the same reward model of the environment (Fig. 2A, ‘SRPE & URPE’ contextual drift), leading to increased pattern similarity in the contexts of those items. We compared the output of this model to one that only included the URPE drift and one that relied only on a static drift value, excluding both RPE modulators (Fig. 2A).

Temporal-order memory simulation

During memory encoding, we presented 32 items to the network (orthogonal 'one-hot' unit vectors) which included three large URPE, model-update items that indicated the start of a new reward context. These model-update event boundaries occurred after a sequence of eight items, similar to the structure of previous paradigms (Clewett et al., 2020; Rouhani et al., 2020). To simulate a chaining process during memory retrieval, we depended only on the model's episodic (versus semantic) route given order memory's dependence on episodic memory mechanisms (Davachi & DuBrow, 2015); for model details, see (Rouhani et al., 2020). The retrieval process is initiated by priming the network with each item included in a tested pair, one at a time, after which the network engages in a recall period governed by a leaky, competitive accumulation process (Usher & McClelland, 2001). We simulated this process 1000 times for each item within a pair using the same tested pairs in (Rouhani et al., 2020) and determined the number of successful retrievals of the other (target) item. We further tracked the number of intervening items (experienced between the tested items during encoding) that were retrieved by the network before successful or unsuccessful retrieval of the target item.

All parameters of the original model (Rouhani et al., 2020) were implemented, with the exception of the contextual drift. For the 'SRPE and URPE' contextual-drift model, we decreased the standard drift parameter (which begins at the original value, $\beta = 0.6$) for each subsequent item within a context, and retained the higher-drift parameter of the large-URPE item (β*-model update* = 0.8). The value of this SRPE trial-by-trial decrement in drift was determined by simulating results ranging from 0 to 0.09 (in 0.01 increments), 1000 times each, and selecting the value that best captured the qualitative pattern of behavioral results (0.04, see 'Simulation results' below). The qualitative fit was determined by matching the relative difference in the means of order recall for each condition with that observed in behavior. We next compared the simulations of this model to two different models. The first model only included the URPE, model-update increase in contextual drift (β*-model update* = 0.8, otherwise $\beta = 0.6$). The second model excluded both RPE modulators, instead implementing a static drift of 0.75 (consistent with the original fit values of this parameter (Polyn et al., 2009); Fig. 2A).

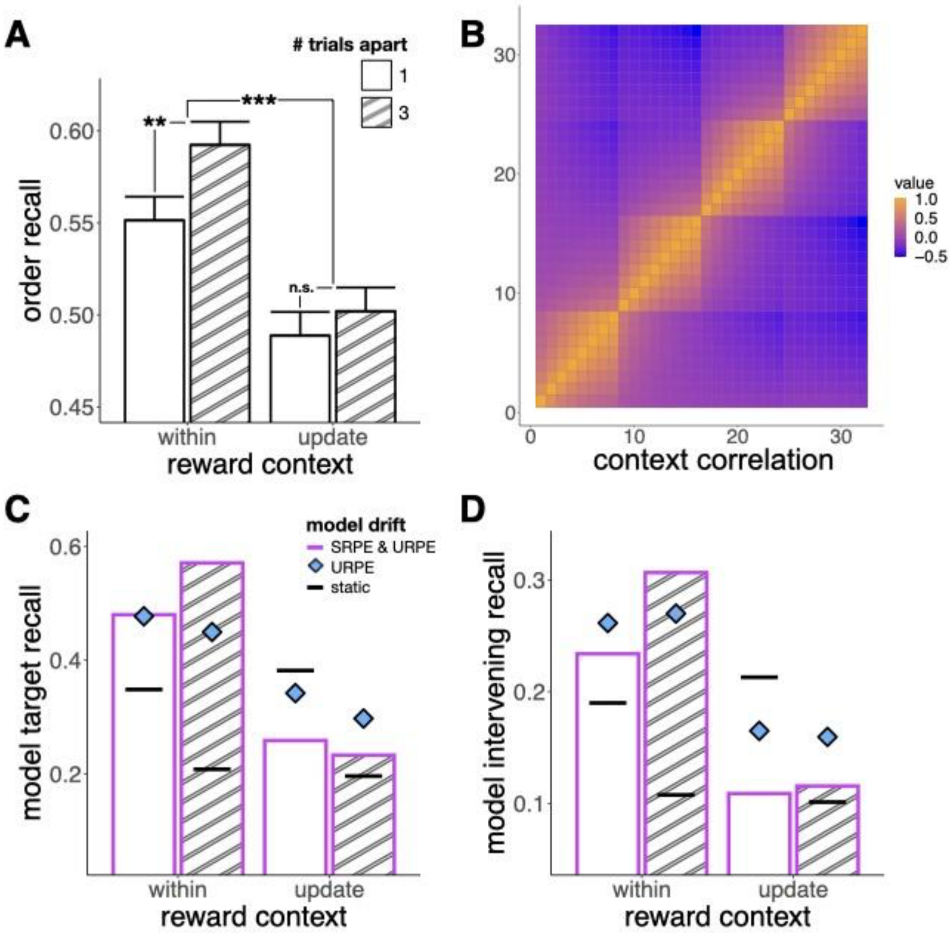


Figure 3. Temporal-order memory in behavior and model simulations. **A**. Behavior: Temporal-order memory results in Rouhani et al., 2020 (across Experiment 4 and its replication). Participants were asked to indicate which of two presented scenes occurred first; scene pairs were either within the same reward context or across large URPE model-update outcomes ('within' versus 'update') and varied in the number of intervening items at encoding (1 versus 3-trials apart). Order memory for items within the same reward context was better overall and for pairs that had been more trials apart at encoding (more intervening items), whereas order memory was impaired across all pairs that crossed a model update, without similar improvements for more distant pairs. ***p<0.001, **p<0.01, **n.s.** p>0.10. **B**. Model simulations: correlations between the context vectors after encoding. The sharp increase in contextual drift during model-update outcomes created representational structure: items belonging to the same underlying reward context were more similar to each other than those that crossed a reward context (or model) update. **C**. Model simulations: Proportion of successful target retrievals. A model that increased contextual drift during model-update items (reflecting URPE signals at outcome) and decreased the contextual drift within a reward context (reflecting increasing SRPE signals at cue) predicted the behavioral pattern of results in (A). A model that only included the URPE component (diamond points) captured worse recall of items that crossed an event boundary, but did not replicate better recall of more-distant items within the same reward context. A model without either reward prediction error component (static drift, black lines) did not predict worse recall for boundary-spanning pairs nor improved memory for within-context items that were further apart (predicted the opposite pattern). **D**. Model simulations: Proportion of intervening item recall during successful target retrievals. We found that intervening-item reactivation predicted successful recall of the target item.

Simulation results

We found that increased contextual drift at model-update items, along with its incremental decrease within a reward context, predicted our pattern of behavioral results (Fig. 3A,C). As before, a higher-value drift during large URPE, model-update outcomes caused pattern separation in the contexts of experienced rewards, here representing a change in the means of the underlying reward distribution (Rouhani et al., 2020). Consequently, when testing pairs that crossed a model update, items were less likely to episodically retrieve each other, predicting worse order memory (Fig. 3C).

On the other hand, a theoretical SRPE that diminished contextual drift within a reward context – beginning with the original drift of 0.6 and decreasing by 0.04 for every subsequent item – led to better episodic retrieval of the target item. This enhancement increased for pairs that had been further apart from each other during encoding (1 vs. 3-trials apart, Fig. 3C), mirroring behavioral results (Fig. 3A). To note, model retrieval proportions (Fig. 3C) do not account for baseline chance performance, precluding a direct comparison of those numerical values to behavior (Fig. 3A). We also do not include statistics in our model simulations, as the 1000 simulations run for each item within a pair yielded reliable output, and statistical comparison between large numbers of simulations (24000 total simulations) reflect inflated significance values (all reported differences were $p<0.0001$).

We compared these results to a model that only included the URPE drift and one that excluded RPE drift altogether (static model). While the URPE model captured the retrieval impairment for context-spanning pairs, it did not predict improving recall for more distant within-context pairs (Fig. 3C, diamond points). Worse, the static-drift model did not predict any differences between pairs within or across reward contexts. Moreover, and to a larger extent than the URPE-drift model, the static-drift model predicted the opposite results for more distant, within-context pairs such that items that were further apart during encoding were less likely, rather than more likely, to be retrieved (Fig. 3C, black lines). This finding confirms that a decreasing drift (SRPE & URPE contextual drift) versus a static drift within a reward context (URPE and static contextual drifts) allows more items to cue each other through more similar contexts during recall.

We further tested whether associative chaining (DuBrow & Davachi, 2013, 2014, 2016), represented by network reactivation of intervening items, predicted the subsequent retrieval of target items as well as better recall of more distant within-context items. First, we indeed found intervening-item reactivation to predict subsequent retrieval of the target item within and across all pair types and contextual-drift models (all ps < 0.001). Furthermore, when examining simulations with successful target retrievals, pair types and contextual-drift models led to different proportions of intervening-item retrieval (Fig. 3D), mirroring the pattern of model results in order memory (Fig. 3C).

More specifically, when implementing SRPE & URPE contextual drift, intervening items were more likely to be retrieved for pairs within versus across reward contexts. Moreover, within a reward context, pairs that were encountered more trials apart were more likely to retrieve any of the (three) intervening items. An associative chaining process, wherein intervening items are more likely to be recalled, may therefore support better temporal-order memory for more distant items within a stable context. This effect was not observed for pairs that crossed a model-update outcome, whose higher contextual drift generated more dissimilarity between the contexts of tested items, precluding the retrieval of intervening and target items.

Simulation discussion

In this simulation, we examined how theoretical SRPE signals at reward-predictive cue and URPE signals at reward outcome may govern the contextual drift associated with those items to predict patterns in temporal-order memory. We hypothesized that with more learning, larger positive SRPEs, representing the value of that experience, would decrease the contextual drift and increase pattern similarity within a reward context. Indeed, we found this decreased drift better predicted the episodic retrieval of more distant pairs that occurred in the same reward context. In contrast, we hypothesized that large URPEs that indicate a change in the underlying reward distribution (model-update outcomes) would increase contextual drift. We found this manipulation to pattern separate the contexts of items that occurred in different reward contexts, leading to impaired episodic retrieval of items that crossed large URPE, model-update outcomes.

Additionally, we found that a temporal memory mechanism relying on associative chaining (DuBrow et al., 2017; DuBrow & Davachi, 2013, 2014, 2016) versus distance theories (Friedman, 1993; Pu et al., 2022; Rouhani et al., 2020) supported prior behavioral results.

Consistent with experimental work, we observed that the reactivation of intervening items predicted the episodic retrieval of target items across all pair types (DuBrow & Davachi, 2014). Importantly, however, the likelihood of intervening-item reactivation differed between pair types to explain behavioral patterns, demonstrating its key role in supporting the mnemonic sequencing of items. Future empirical studies could more directly compare whether an associative-chaining account of temporal-order memory – relying on the reactivation of intervening items during recall (DuBrow & Davachi, 2013, 2014, 2016) – versus a distance account – relying on representational distance (Jenkins & Ranganath, 2016; Liu et al., 2022) or the reactivation of initial contexts at event boundaries (Pu et al., 2022) – supports neural and behavioral signatures of temporal-order memory within and across contexts.

Our theoretical model presents limitations and avenues for further development. First, while the model relies on the episodic routes of the CMR to encode and retrieve items, it does not explicitly reconstruct item order. Future work could test SRPE integration versus URPE segmentation by leveraging models that explicitly reconstruct temporal order (Franklin et al., 2020). Additionally, in our model, the dynamics in contextual drift were theoretically associated with RPE signals and did not reflect the empirical RPE values of each trial during learning. For example, we assumed a single, linear decrease in SRPE contextual drift, whereas the rate of learning varies between individuals and reward environments, suggesting there may be greater variability in the form and degree of this decrease. Although our model does not differentiate SRPE effects in high- versus low-reward environments, higher reward motivation, with larger SRPEs, may further decrease temporal drift to predict better order memory. On the flip side, decreasing motivation may impair order memory, potentially explaining the worse ordering of items encountered later in a context (Pu et al., 2022). Future studies should examine the influence of motivation on contextual similarity and subsequent order memory.

The increase in contextual drift during large URPE, model-update outcomes was also uniform in our model, whereas these outcomes can vary in magnitude. While the specific magnitude of model-update outcomes did not appear to further influence temporal-order memory in behavior (Rouhani et al., 2020), the changes in the underlying reward distributions in this task were less noisy and uncertain than in real-world scenarios. Our model could incorporate empirical RPEs that reflect individual learning trajectories and trial-by-trial uncertainty in the detection of a new reward context. It could also be implemented in more naturalistic tasks to potentially capture the richness and variability of different encoding contexts. Lastly, given that drift appears to occur at multiple timescales in the brain (Antony, Liu, et al., 2023; Mau et al., 2018; Rubin et al., 2015; Tsao et al., 2018), our model could be developed to describe how RPEs induce changes at different timescales to support the observed memory patterns.

Discussion

Prediction errors govern how we learn and what we remember in laboratory experiments and in the real world (Antony, Van Dam, et al., 2023; Bein et al., 2023; Rouhani, Niv, et al., 2023; Rouhani, Stanley, et al., 2023). In our computational model, we highlight how two prediction error signals, the positive SRPE (value signal) at reward cue and the URPE (model-update signal) at reward outcome, may differentially integrate versus segment rewarding experiences in memory.

We propose that a positive SRPE that builds with stronger reward expectations at reward cue, linked to increased DA firing from the midbrain, may increase the contextual similarity of those experiences to support temporal-order memory within a reward context. Conversely, large model-update URPEs at reward outcome, associated with DA and NE signals from the LC, may decrease the contextual similarity of temporally-adjacent experiences to create separate reward contexts in memory. These RPE effects were simulated in a variant of the CMR model (Rouhani et al., 2020), which predicted the pattern of order memory through an associative chaining process. Here, greater contextual similarity (produced by a SRPE) predicted increased reactivation of intervening items to enhance retrieval of more distant items from the same reward environment. By contrast, the break in context (produced by a URPE) decreased the reactivation of intervening items and impaired retrieval of items that crossed it.

We note that the extent of (SRPE) pattern similarity versus (URPE) pattern separation may differentially influence memory for generalized, value-based information versus specific details of the event itself, respectively. This is consistent with midbrain DA's role in memory generalization versus LC-modulated memory for event details (Duszkiewicz et al., 2019). Greater hippocampal pattern similarity can moreover facilitate (DuBrow & Davachi, 2014) and interfere with temporal-order memory (Jenkins & Ranganath, 2016), raising the question as to when contextual similarity helps guide versus impairs successful episodic retrieval. Future work could examine the relationships between RPEs, contextual similarity in the hippocampus, and their effects on more generalized versus detailed episodic memory for rewarding experiences.

While we focused on reward learning signals, these prediction error effects may not be exclusive to rewarding outcomes. For example, we expect the effects of URPEs to generalize to non-reward domains, consistent with episodic memory signatures of event boundaries (Clewett et al., 2020; DuBrow & Davachi, 2013; Heusser et al., 2018). For example, other elicitations of arousal, including emotional stimuli (Clewett et al., 2014; Clewett & McClay, 2024; McClay et al., 2023) or task switching (Wang & Egner, 2022), have been shown to elicit segmentation effects in memory. Additionally, the building of SRPEs reflects strengthening expectations, which may be relevant to the formation of any cognitive model (Langdon et al., 2018; Sharpe, Batchelor, et al., 2017; Sharpe, Chang, et al., 2017). Nevertheless, it is likely that the affective domain of the SRPE (e.g., positive, negative or neutral) would produce different mnemonic effects given a well established body of work showing the distinct influences of positive and negative emotion on the quality and quantity of memory (Clewett & Murty, 2019; Murty & Alison Adcock, 2017; Palombo & Cocquyt, 2020; Rouhani, Niv, et al., 2023; Williams et al., 2022). Recent work supports this idea, demonstrating that positive emotions tend to bind and compress memories, whereas negative emotions tend to segment and separate adjacent events in memory (McClay et al., 2023).

The effects of building negative (versus positive) SRPEs are moreover relevant to clinical disorders. For instance, post-traumatic stress disorder, marked by intrusive and recurrent traumatic memories, has been associated with distinct arousal and hippocampal responses to threat (Tanriverdi et al., 2022), which have been recently suggested to reflect disruptions in model-update processes (Cisler et al., 2024). Negative SRPEs may further engage LC-arousal systems to segment rather than integrate memory across experience (Clewett et al., 2014; Clewett & McClay, 2024; McClay et al., 2023). This work demonstrates that valenced expectations influence memory organization in a manner not yet examined in our model, with implications for the maladaptive processing of negative experience.

In sum, we propose that RPEs, quantifying the valence and surprise of reward outcomes, may be critical modulators of both event integration and segmentation, consistent with putative neural signals that interact with the hippocampus to support episodic memory.

References

Antony, J. W., Hartshorne, T. H., Pomeroy, K., Gureckis, T. M., Hasson, U., McDougle, S. D., & Norman, K. A. (2021). Behavioral, Physiological, and Neural Signatures of Surprise during Naturalistic Sports Viewing. *Neuron*, *109*(2), 377–390.e7.

Antony, J. W., Liu, X. L., Zheng, Y., Ranganath, C., & O'Reilly, R. C. (2023). Memory out of context: Spacing effects and decontextualization in a computational model of the medial temporal lobe. In *bioRxiv* (p. 2022.12.01.518703). https://doi.org/10.1101/2022.12.01.518703

Antony, J. W., Van Dam, J., Massey, J. R., Barnett, A. J., & Bennion, K. A. (2023). Long-term, multi-event surprise correlates with enhanced autobiographical memory. *Nature Human Behaviour*, *7*(12), 2152–2168.

Bakker, A., Kirwan, C. B., Miller, M., & Stark, C. E. L. (2008). Pattern separation in the human hippocampal CA3 and dentate gyrus. *Science*, *319*(5870), 1640–1642.

Baldassano, C., Chen, J., Zadbood, A., Pillow, J. W., Hasson, U., & Norman, K. A. (2017). Discovering Event Structure in Continuous Narrative Perception and Memory. *Neuron*, *95*(3), 709–721.e5.

Barto, A. G. (1995). Adaptive critic and the basal ganglia. In J. C. Houk, J. L. Davis, & D. G. Beiser (Eds.), *Models of information processing in the basal ganglia* (p. 215). MIT press.

Bein, O., Duncan, K., & Davachi, L. (2020). Mnemonic prediction errors bias hippocampal states. *Nature Communications*, *11*(1), 3451.

Bein, O., Gasser, C., Amer, T., Maril, A., & Davachi, L. (2023). Predictions transform memories: How expected versus unexpected events are integrated or separated in memory. *Neuroscience and Biobehavioral Reviews*, 105368.

Ben-Yakov, A., & Dudai, Y. (2011). Constructing realistic engrams: poststimulus activity of hippocampus and dorsal striatum predicts subsequent episodic memory. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *31*(24), 9032–9042.

Ben-Yakov, A., Eshel, N., & Dudai, Y. (2013). Hippocampal immediate poststimulus activity in the encoding of consecutive naturalistic episodes. *Journal of Experimental Psychology. General*, *142*(4), 1255–1263.

Ben-Yakov, A., & Henson, R. N. (2018). The Hippocampal Film Editor: Sensitivity and Specificity to Event Boundaries in Continuous Experience. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *38*(47), 10057–10068.

Bladon, J. H., Sheehan, D. J., De Freitas, C. S., & Howard, M. W. (2019). In a Temporally Segmented Experience Hippocampal Neurons Represent Temporally Drifting Context But Not Discrete Segments. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *39*(35), 6936–6952.

Bornstein, A. M., & Norman, K. A. (2017). Reinstated episodic context guides sampling-based decisions for reward. *Nature Neuroscience*, *20*(7), 997–1003.

Bouret, S., & Sara, S. J. (2005). Network reset: a simplified overarching theory of locus coeruleus noradrenaline function. *Trends in Neurosciences*, *28*(11), 574–582.

Caplan, J. B., Shafaghat Ardebili, A., & Liu, Y. S. (2022). Chaining models of serial recall can produce positional errors. *Journal of Mathematical Psychology*, *109*, 102677.

Cisler, J. M., Dunsmoor, J. E., Fonzo, G. A., & Nemeroff, C. B. (2024). Latent-state and model-based learning in PTSD. *Trends in Neurosciences*. https://doi.org/10.1016/j.tins.2023.12.002

Clewett, D., DuBrow, S., & Davachi, L. (2019). Transcending time in the brain: How event memories are constructed from experience. *Hippocampus*, *29*(3), 162–183.

Clewett, D., Gasser, C., & Davachi, L. (2020). Pupil-linked arousal signals track the temporal organization of events in memory. In *Nature Communications* (Vol. 11, Issue 1). https://doi.org/10.1038/s41467-020-17851-9

Clewett, D., & McClay, M. (2024). Emotional arousal lingers in time to bind discrete episodes in memory. *Cognition & Emotion*, 1–20.

Clewett, D., & Murty, V. P. (2019). Echoes of emotions past: How neuromodulators determine what we recollect. *eNeuro*, *6*(2). https://doi.org/10.1523/ENEURO.0108-18.2019

Clewett, D., Schoeke, A., & Mather, M. (2014). Locus coeruleus neuromodulation of memories encoded during negative or unexpected action outcomes. *Neurobiology of Learning and Memory*, *111*, 65–70.

Dahl, M. J., Kulesza, A., Werkle-Bergner, M., & Mather, M. (2023). Declining locus coeruleus–dopaminergic and noradrenergic modulation of long-term memory in aging and Alzheimer's disease. *Neuroscience and Biobehavioral Reviews*, *153*, 105358.

Davachi, L., & DuBrow, S. (2015). How the hippocampus preserves order: the role of prediction and context. *Trends in Cognitive Sciences*, *19*(2), 92–99.

Dimsdale-Zucker, H. R., Montchal, M. E., Reagh, Z. M., Wang, S.-F., Libby, L. A., & Ranganath, C. (2022). Representations of Complex Contexts: A Role for Hippocampus. *Journal of Cognitive Neuroscience*, *35*(1), 90–110.

DuBrow, S., & Davachi, L. (2013). The influence of context boundaries on memory for the sequential order of events. *Journal of Experimental Psychology. General*, *142*(4), 1277–1286.

DuBrow, S., & Davachi, L. (2014). Temporal memory is shaped by encoding stability and intervening item reactivation. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *34*(42), 13998–14005.

DuBrow, S., & Davachi, L. (2016). Temporal binding within and across events. *Neurobiology of Learning and Memory*, *134 Pt A*, 107–114.

DuBrow, S., Rouhani, N., Niv, Y., & Norman, K. A. (2017). Does mental context drift or shift? *Current Opinion in Behavioral Sciences*, *17*, 141–146.

Duncan, K., Ketz, N., Inati, S. J., & Davachi, L. (2012). Evidence for area CA1 as a match/mismatch detector: a high-resolution fMRI study of the human hippocampus. *Hippocampus*, *22*(3), 389–398.

Duszkiewicz, A. J., McNamara, C. G., Takeuchi, T., & Genzel, L. (2019). Novelty and Dopaminergic Modulation of Memory Persistence: A Tale of Two Systems. *Trends in Neurosciences*, *42*(2), 102–114.

Eichenbaum, H., & Cohen, N. J. (2004). *From Conditioning to Conscious Recollection: Memory Systems of the Brain*. Oxford University Press, USA.

Franklin, N. T., Norman, K. A., Ranganath, C., Zacks, J. M., & Gershman, S. J. (2020). Structured Event Memory: A neuro-symbolic model of event cognition. *Psychological Review*, *127*(3), 327–361.

Friedman, W. J. (1993). Memory for the time of past events. *Psychological Bulletin*, *113*(1), 44–66.

Friedman, W. J. (2004). Time in autobiographical memory. *Social Cognition*, *22*(5), 591–605.

Geva, N., Deitch, D., Rubin, A., & Ziv, Y. (2023). Time and experience differentially affect distinct aspects of hippocampal representational drift. *Neuron*, *111*(15), 2357–2366.e5.

Grella, S. L., Gomes, S. M., Lackie, R. E., Renda, B., & Marrone, D. F. (2021). Norepinephrine as a spatial memory reset signal. *Behavioural Pharmacology*, *32*(7), 531–548.

Heusser, A. C., Ezzyat, Y., Shiff, I., & Davachi, L. (2018). Perceptual boundaries cause mnemonic trade-offs between local boundary processing and across-trial associative binding. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *44*(7), 1075–1090.

Hintzman, D. L. (2002). Context matching and judgments of recency. *Psychonomic Bulletin & Review*, *9*(2), 368–374.

Horner, A. J., Bisby, J. A., Wang, A., Bogus, K., & Burgess, N. (2016). The role of spatial boundaries in shaping long-term event representations. *Cognition*, *154*, 151–164.

Horwath, E. A., Rouhani, N., DuBrow, S., & Murty, V. P. (2023). Value restructures the organization of free recall. *Cognition*, *231*, 105315.

Huang, R., & Clewett, D. (2024). The Locus Coeruleus: Where Cognitive and Emotional Processing Meet the Eye. In M. H. Papesh & S. D. Goldinger (Eds.), *Modern Pupillometry: Cognition, Neuroscience, and Practical Applications* (pp. 3–75). Springer International Publishing.

Jang, A. I., Nassar, M. R., Dillon, D. G., & Frank, M. J. (2019). Positive reward prediction errors during decision-making strengthen memory encoding. *Nature Human Behaviour*, *3*(7), 719–

732.

Jenkins, L. J., & Ranganath, C. (2016). Distinct neural mechanisms for remembering when an event occurred. *Hippocampus*, *26*(5), 554–559.

Jeong, H., Taylor, A., Floeder, J. R., Lohmann, M., Mihalas, S., Wu, B., Zhou, M., Burke, D. A., & Namboodiri, V. M. K. (2022). Mesolimbic dopamine release conveys causal associations. *Science*, eabq6740.

Jordan, R. (2023). The locus coeruleus as a global model failure system. *Trends in Neurosciences*, *0*(0). https://doi.org/10.1016/j.tins.2023.11.006

Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between Pupil Diameter and Neuronal Activity in the Locus Coeruleus, Colliculi, and Cingulate Cortex. *Neuron*, *89*(1), 221–234.

Kafkas, A. (2021). Encoding-linked pupil response is modulated by expected and unexpected novelty: Implications for memory formation and neurotransmission. *Neurobiology of Learning and Memory*, *180*, 107412.

Kempadoo, K. A., Mosharov, E. V., Choi, S. J., Sulzer, D., & Kandel, E. R. (2016). Dopamine release from the locus coeruleus to the dorsal hippocampus promotes spatial learning and memory. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(51), 14835–14840.

Khatib, D., Ratzon, A., Sellevoll, M., Barak, O., Morris, G., & Derdikman, D. (2023). Active experience, not time, determines within-day representational drift in dorsal CA1. *Neuron*, *0*(0). https://doi.org/10.1016/j.neuron.2023.05.014

Kim, H. R., Malik, A. N., Mikhael, J. G., Bech, P., Tsutsui-Kimura, I., Sun, F., Zhang, Y., Li, Y., Watabe-Uchida, M., Gershman, S. J., & Uchida, N. (2020). A Unified Framework for Dopamine Signals across Timescales. *Cell*. https://doi.org/10.1016/j.cell.2020.11.013

Langdon, A. J., Sharpe, M. J., Schoenbaum, G., & Niv, Y. (2018). Model-based predictions for dopamine. *Current Opinion in Neurobiology*, *49*, 1–7.

Lee, H., & Chen, J. (2022). Predicting memory from the network structure of naturalistic events. *Nature Communications*, *13*(1), 4235.

Lisman, J. E., & Grace, A. A. (2005). The hippocampal-VTA loop: controlling the entry of information into long-term memory. *Neuron*, *46*(5), 703–713.

Liu, C., Ye, Z., Chen, C., Axmacher, N., & Xue, G. (2022). Hippocampal Representations of Event Structure and Temporal Context during Episodic Temporal Order Memory. *Cerebral Cortex* , *32*(7), 1520–1534.

Mau, W., Sullivan, D. W., Kinsky, N. R., Hasselmo, M. E., Howard, M. W., & Eichenbaum, H. (2018). The Same Hippocampal CA1 Population Simultaneously Codes Temporal Information over Multiple Timescales. *Current Biology: CB*, *28*(10), 1499–1508.e4.

McClay, M., Sachs, M. E., & Clewett, D. (2023). Dynamic emotional states shape the episodic structure of memory. *Nature Communications*, *14*(1), 6533.

Montague, P. R., Dayan, P., & Sejnowski, T. J. (1996). A framework for mesencephalic dopamine systems based on predictive Hebbian learning. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *16*(5), 1936–1947.

Murty, V. P., & Alison Adcock, R. (2017). Distinct Medial Temporal Lobe Network States as Neural Contexts for Motivated Memory Formation. In D. E. Hannula & M. C. Duff (Eds.), *The Hippocampus from Cells to Systems: Structure, Connectivity, and Functional Contributions to Memory and Flexible Cognition* (pp. 467–501). Springer International Publishing.

Nassar, M. R., McGuire, J. T., Ritz, H., & Kable, J. W. (2019). Dissociable Forms of Uncertainty-Driven Representational Change Across the Human Brain. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *39*(9), 1688–1698.

Nassar, M. R., Rumsey, K. M., Wilson, R. C., Parikh, K., Heasly, B., & Gold, J. I. (2012). Rational regulation of learning dynamics by pupil-linked arousal systems. *Nature Neuroscience*, *15*(7), 1040–1046.

Nieuwenhuis, S., Gilzenrat, M. S., Holmes, B. D., & Cohen, J. D. (2005). The role of the locus coeruleus in mediating the attentional blink: a neurocomputational theory. *Journal of Experimental Psychology. General*, *134*(3), 291–307.

O'Reilly, J. X., Schüffelgen, U., Cuell, S. F., Behrens, T. E. J., Mars, R. B., & Rushworth, M. F. S. (2013). Dissociable effects of surprise and model update in parietal and anterior cingulate cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(38), E3660–E3669.

Palombo, D. J., & Cocquyt, C. (2020). Emotion in Context: Remembering When. *Trends in Cognitive Sciences*, *0*(0). https://doi.org/10.1016/j.tics.2020.05.017

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*(1), 129–156.

Pu, Y., Kong, X.-Z., Ranganath, C., & Melloni, L. (2022). Event boundaries shape temporal organization of memory by resetting temporal context. *Nature Communications*, *13*(1), 622.

Reagh, Z. M., Delarazan, A. I., Garber, A., & Ranganath, C. (2020). Aging alters neural activity at event boundaries in the hippocampus and Posterior Medial network. *Nature Communications*, *11*(1), 3980.

Rescorla, R., & Wagner, A. (1972). A theory of Pavlovian conditoining: 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). Appleton-Century-Crofts.

Rouhani, N., & Niv, Y. (2021). Signed and unsigned reward prediction errors dynamically enhance learning and memory. *eLife*, *10*. https://doi.org/10.7554/eLife.61077

Rouhani, N., Niv, Y., Frank, M. J., & Schwabe, L. (2023). Multiple routes to enhanced memory for emotionally relevant events. *Trends in Cognitive Sciences*, *27*(9), 867–882.

Rouhani, N., Norman, K. A., & Niv, Y. (2018). Dissociable effects of surprising rewards on learning and memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *44*(9), 1430–1443.

Rouhani, N., Norman, K. A., Niv, Y., & Bornstein, A. M. (2020). Reward prediction errors create event boundaries in memory. *Cognition*, *203*, 104269.

Rouhani, N., Stanley, D., COVID-Dynamic Team, & Adolphs, R. (2023). Collective events and individual affect shape autobiographical memory. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(29), e2221919120.

Rubin, A., Geva, N., Sheintuch, L., & Ziv, Y. (2015). Hippocampal ensemble dynamics timestamp events in long-term memory. *eLife*, *4*. https://doi.org/10.7554/eLife.12247

Sales, A. C., Friston, K. J., Jones, M. W., Pickering, A. E., & Moran, R. J. (2019). Locus Coeruleus tracking of prediction errors optimises cognitive flexibility: An Active Inference model. *PLoS Computational Biology*, *15*(1), e1006267.

Sara, S. J. (2009). The locus coeruleus and noradrenergic modulation of cognition. *Nature Reviews. Neuroscience*, *10*(3), 211–223.

Sara, S. J., & Bouret, S. (2012). Orienting and reorienting: the locus coeruleus mediates cognition through arousal. *Neuron*, *76*(1), 130–141.

Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, *275*(5306), 1593–1599.

Sharpe, M. J., Batchelor, H. M., & Schoenbaum, G. (2017). Preconditioned cues have no value. *eLife*, *6*, 1–9.

Sharpe, M. J., Chang, C. Y., Liu, M. A., Batchelor, H. M., Mueller, L. E., Jones, J. L., Niv, Y., & Schoenbaum, G. (2017). Dopamine transients are sufficient and necessary for acquisition of model-based associations. *Nature Neuroscience*, *20*(5), 735–742.

Shimamura, A. P., Janowsky, J. S., & Squire, L. R. (1990). Memory for the temporal order of events in patients with frontal lobe lesions and amnesic patients. *Neuropsychologia*, *28*(8), 803–813.

Shin, Y. S., & DuBrow, S. (2021). Structuring Memory Through Inference-Based Event Segmentation. *Topics in Cognitive Science*, *13*(1), 106–127.

Silva, M., Baldassano, C., & Fuentemilla, L. (2019). Rapid Memory Reactivation at Movie Event Boundaries Promotes Episodic Encoding. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *39*(43), 8538–8548.

Sols, I., DuBrow, S., Davachi, L., & Fuentemilla, L. (2017). Event Boundaries Trigger Rapid Memory Reinstatement of the Prior Events to Promote Their Representation in Long-Term

Memory. *Current Biology: CB*, *27*(22), 3499–3504.e4.

Stanek, J. K., Dickerson, K. C., Chiew, K. S., Clement, N. J., & Adcock, R. A. (2019). Expected Reward Value and Reward Uncertainty Have Temporally Dissociable Effects on Memory Formation. *Journal of Cognitive Neuroscience*, *31*(10), 1443–1454.

Swallow, K. M., Broitman, A. W., Riley, E., & Turker, H. B. (2022). Grounding the Attentional Boost Effect in Events and the Efficient Brain. *Frontiers in Psychology*, *13*, 892416.

Swallow, K. M., & Jiang, Y. V. (2010). The Attentional Boost Effect: Transient increases in attention to one task enhance performance in a second task. *Cognition*, *115*(1), 118–132.

Takeuchi, T., Duszkiewicz, A. J., Sonneborn, A., Spooner, P. A., Yamasaki, M., Watanabe, M., Smith, C. C., Fernández, G., Deisseroth, K., Greene, R. W., & Morris, R. G. M. (2016). Locus coeruleus and dopaminergic consolidation of everyday memory. *Nature*, *537*(7620), 357–362.

Tanriverdi, B., Gregory, D. F., Olino, T. M., Ely, T. D., Harnett, N. G., van Rooij, S. J. H., Lebois, L. A. M., Seligowski, A. V., Jovanovic, T., Ressler, K. J., House, S. L., Beaudoin, F. L., An, X., Neylan, T. C., Clifford, G. D., Linnstaedt, S. D., Germine, L. T., Bollen, K. A., Rauch, S. L., … Murty, V. P. (2022). Hippocampal Threat Reactivity Interacts with Physiological Arousal to Predict PTSD Symptoms. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*. https://doi.org/10.1523/JNEUROSCI.0911-21.2022

Tompary, A., & Davachi, L. (2020). Consolidation Promotes the Emergence of Representational Overlap in the Hippocampus and Medial Prefrontal Cortex. *Neuron*, *105*(1), 199–200.

Tsao, A., Sugar, J., Lu, L., Wang, C., Knierim, J. J., Moser, M.-B., & Moser, E. I. (2018). Integrating time from experience in the lateral entorhinal cortex. *Nature*, *561*(7721), 57–62.

Tubridy, S., & Davachi, L. (2011). Medial temporal lobe contributions to episodic sequence encoding. *Cerebral Cortex* , *21*(2), 272–280.

Usher, M., & McClelland, J. L. (2001). The time course of perceptual choice: the leaky, competing accumulator model. *Psychological Review*, *108*(3), 550–592.

Wang, Y. C., & Egner, T. (2022). Switching task sets creates event boundaries in memory. *Cognition*, *221*, 104992.

Wang, Y. C., & Egner, T. (2023). Target detection does not influence temporal memory. *Attention, Perception & Psychophysics*, *85*(6), 1936–1948.

Williams, S. E., Ford, J. H., & Kensinger, E. A. (2022). The power of negative and positive episodic memories. *Cognitive, Affective & Behavioral Neuroscience*, *22*(5), 869–903.

Yu, A. J., & Dayan, P. (2005). Uncertainty, neuromodulation, and attention. *Neuron*, *46*(4), 681–692.

Zacks, J. M., Speer, N. K., Swallow, K. M., Braver, T. S., & Reynolds, J. R. (2007). Event perception: A mind-brain perspective. In *Psychological Bulletin* (Vol. 133, Issue 2, pp. 273–293). https://doi.org/10.1037/0033-2909.133.2.273

Zhao, S., Chait, M., Dick, F., Dayan, P., Furukawa, S., & Liao, H.-I. (2019). Pupil-linked phasic arousal evoked by violation but not emergence of regularity within rapid sound sequences. *Nature Communications*, *10*(1), 4030.

Zheng, J., Schjetnan, A. G. P., Yebra, M., Gomes, B. A., Mosher, C. P., Kalia, S. K., Valiante, T. A., Mamelak, A. N., Kreiman, G., & Rutishauser, U. (2022). Neurons detect cognitive boundaries to structure episodic memories in humans. *Nature Neuroscience*, *25*(3), 358–368.