

Time after Time: Preserving Temporal Memories When Experiences Repeat

Futing Zou^{ID} and Brice A. Kuhl

Abstract

■ Remembering when events occur in time is fundamental to episodic memory. Yet, many experiences repeat over time creating the potential for interference when attempting to recall temporally specific memories. Here, we argue that temporal memories are protected, in part, by reinstatement of temporal context information that is triggered by stimulus repetitions. We motivate this argument by integrating seminal findings across several distinct literatures and methodologies. Specifically, we consider key insights from foundational behavioral studies of temporal memory, recent

electrophysiological and neuroimaging approaches to measuring memory reinstatement, and computational models that describe how temporal context representations shape memory processes. We also note several open questions concerning how temporal context reinstatement might influence subsequent temporal memory, including potential mediating effects of event spacing and event boundaries. These ideas and questions have the potential to guide future research and, ultimately, to advance theoretical accounts of how we preserve temporal memories. ■

INTRODUCTION

The ability to remember when events occurred in time—temporal memory—is a definitional component of episodic memory (Tulving, 2002). We rely on temporal memory not only to organize our reflections on past experiences but also to guide future behavior. For example, temporal memory is critical for evaluating whether stored food is viable for consumption (nuts cached by a bird or leftover pizza cached by a human), remembering when you last took a medication, or deciding whether it is appropriate to email a colleague with another reminder about an overdue task. Each of these examples highlights a common form of temporal memory—a recency judgment—in which the goal is to estimate the amount of time that has elapsed since an event occurred. Each of these examples also highlights a common challenge to recency judgments: that experiences often repeat across time. For example, your ability to remember the last time you ate pizza may be complicated by memories for the countless other times you have had pizza. As such, trying to recall the specific temporal context in which an experience occurred can be viewed as a memory interference problem (Figure 1A). That is, recalling a specific temporal context represents a more general situation in which a single stimulus has been associated with multiple contexts (Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019).

On the one hand, resolving temporal memory interference could be construed as a retrieval problem—that individual memories are independently encoded across

time and that this interference manifests, and must be sorted out, when specific temporal information needs to be recalled (Mensink & Raaijmakers, 1988). By this account, interference could be resolved via processes that direct attention toward relevant retrieval cues or by comparing automatically retrieved content with goals (Badre & Wagner, 2007). Here, however, we focus on a different possibility: that temporal memory interference can be preempted or reduced via mechanisms that are engaged as memories are encoded. This perspective is motivated by behavioral and neuroimaging studies demonstrating that encoding-related processes can powerfully influence subsequent interference (Antony et al., 2022; Chanales, Dudukovic, Richter, & Kuhl, 2019; Koen & Rugg, 2016; Kuhl, Shah, DuBrow, & Wagner, 2010) and by behavioral studies that have linked encoding-related factors to judgments of temporal recency (Hintzman, 2010).

Here, the specific encoding-related phenomenon that we focus on is the tendency for a stimulus presentation to reinstate prior experiences with that same stimulus—a phenomenon we refer to as repetition-induced reinstatement (Figure 1B). We use this term in a broad sense, inclusive of cognitive concepts such as study-phase retrieval and recursive reminders (Hintzman, 2010) as well as neuroimaging and electrophysiological measures of neural reinstatement (Danker & Anderson, 2010). Indeed, we specifically advocate for the idea that there is a need for better integration of behavioral and neural evidence linking stimulus repetitions, reinstatement, and temporal memory.

University of Oregon

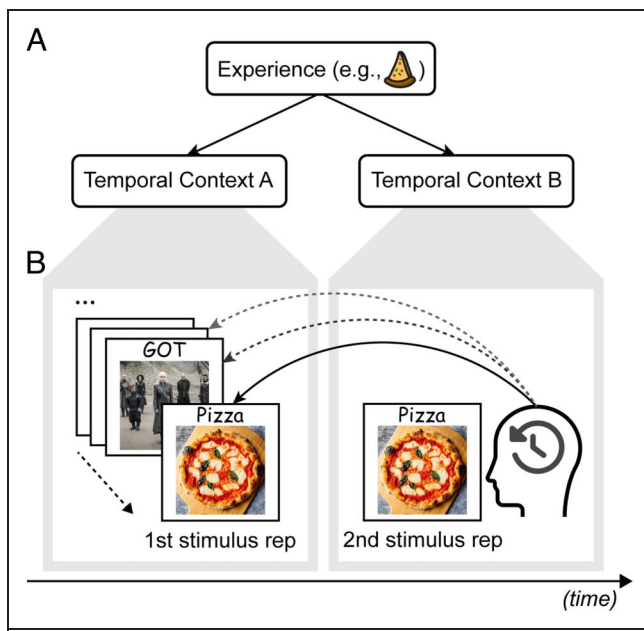


Figure 1. Schematic illustration of stimulus repetition (rep) across temporal contexts. (A) When an experience is repeated across time (e.g., eating pizza from a favorite restaurant), the experience becomes associated with multiple temporal contexts. This has the potential to create interference when later trying to recall a specific temporal episode. (B) When a stimulus repeats in a new temporal context, this may trigger reinstatement of the prior temporal context in which the stimulus was encoded (e.g., the show you were watching the last time you had pizza for dinner).

In the following sections, we first consider behavioral evidence motivating the idea that stimulus repetitions trigger reinstatement, we next consider neural/neuroimaging evidence that stimulus repetitions reinstate the prior temporal context in which a stimulus was encoded, and then we consider specific ways in which reinstatement may influence subsequent temporal memory. We conclude by considering two factors that potentially mediate the relationship between reinstatement and temporal memory: (1) the spacing, or lag, between stimulus repetitions and (2) whether stimulus repetitions are distributed across event boundaries. Across these sections, we consider relationships between behavioral and neural measures, we highlight several of the important gaps in the literature, and we make explicit suggestions for how the field can achieve a better understanding of the mechanisms that preserve temporal memories when experiences repeat across time.

How Does Stimulus Repetition Influence Judgments of Temporal Recency?

Understanding how repetition of a stimulus influences recency judgments has been the subject of extensive behavioral research and has fundamentally informed theories of episodic memory (Hintzman, 2010). In particular, one of the long-standing debates in the field of episodic

memory concerns whether repetitions of a stimulus involve encoding separate memory traces for each occurrence of the stimulus versus strengthening of the original trace (Hintzman, 2010). Although these perspectives lead to relatively similar predictions about some forms of memory (e.g., recognition and recall), they make very different predictions regarding how repetitions will influence temporal recency judgments. Specifically, although a strength-based account can explain how recency judgments are generated for stimuli encountered once before, it is harder for a strength-based account to explain recency judgments (or at least accurate recency judgments) when a single stimulus has repeated across time. Thus, the fact that human participants are able to form separate temporal memories when a stimulus repeats over time (Yntema & Trask, 1963) has been an important and informative piece of evidence in generating theoretical models of episodic memory.

At the extreme, repetitions of a stimulus could be encoded entirely independently of each other. Indeed, several computational models of episodic memory treat stimulus repetitions as independent (Hintzman, 1988; Mensink & Raaijmakers, 1988). However, a variety of evidence from behavioral studies suggests that even if stimulus repetitions (S1, S2, ...) are encoded as separate memories, they are not necessarily independent (Antony et al., 2022; Begg & Green, 1988). Although this nonindependence could take several forms, of particular interest here is the idea that the encoding of S2 can elicit the reinstatement of S1.

One of the earliest and most elegant behavioral findings motivating the idea of repetition-induced reinstatement came from a study by Hintzman in which participants studied a list of stimuli, some of which repeated (Hintzman & Block, 1973). Participants were later asked to make temporal judgments about these stimuli. When the judgment involved estimating how much time passed between the presentations of two different stimuli, participants were close to chance. In contrast, when the judgment involved estimating how much time passed between two presentations of the same stimulus, participants were much more accurate. Hintzman argued that this benefit of stimulus repetition suggests that the second presentation (S2) reinstated the first presentation (S1), including information about when the first presentation occurred (i.e., its recency relative to S2). By this account, the recency information (S1–S2 lag) was thus incorporated into S2 encoding making it available during the subsequent recency judgments. Similar evidence suggesting a link between reinstatement and subsequent recency judgments has also been observed when S1 and S2 are related, but not identical (Hintzman, Summers, & Block, 1975). Outside the domain of temporal memory, the idea of repetition-induced reinstatement is also motivated by evidence that stimulus repetition has overadditive effects on recognition memory (Begg & Green, 1988), and it has been incorporated in leading theoretical accounts of spacing effects on

memory (i.e., why spaced learning benefits subsequent memory; Siegel & Kahana, 2014).

Although the evidence described above suggests a relatively simple story in which stimulus repetitions benefit subsequent recency judgments and that this benefit can be explained by repetition-induced reinstatement, the story is likely more complicated. For example, there is also evidence that stimulus repetition can bias temporal memory estimates and that the influence of stimulus repetition on temporal memory may interact, in complicated ways, with the temporal interval (lag) between repetitions (Hintzman, 2010; Morton, 1968). We consider potential relationships between lag, reinstatement, and temporal memory later in this article.

Taken together, existing behavioral studies have clearly established that when stimuli repeat across time, encoding-related factors can powerfully influence subsequent judgments of when these experiences occurred. In particular, evidence points to the idea that stimulus repetitions induce a reinstatement of prior experiences that can, at least in some cases, preserve temporally specific memories. However, a fundamental limitation of these behavioral studies is that reinstatement is inferred—it is offered as an account of behavioral findings—as opposed to being directly measured. Although it may be feasible, through clever experimental design, to influence the degree to which repetition-induced reinstatement occurs (Manns, Galloway, & Sederberg, 2015; Jacoby & Wahlheim, 2013) or to generate indirect behavioral measures of reinstatement (DuBrow & Davachi, 2014), we argue that neuroimaging and electrophysiological recordings offer a powerful means for more directly measuring repetition-induced reinstatement. Such measurements have the potential to more precisely capture the specific aspects of an experience that are reinstated (e.g., temporal context information) and, thereby, to better understand precisely how and why repetition-induced reinstatement influences temporal memory.

Neural Measures of Repetition-induced Reinstatement

Thus far, we have reviewed behavioral evidence motivating the idea that when a stimulus is repeated, this can trigger reinstatement of earlier encounters with that stimulus. However, what information, exactly, gets reinstated? For reinstatement to benefit subsequent temporal recency judgments, reinstatement presumably must include some information about when the stimulus was previously encoded. Temporal context models provide a useful framework for conceptualizing and testing these ideas. According to these models, when a stimulus is encoded into memory, it is bound to other stimuli that were recently encountered along with other thoughts, emotions, and so forth that might be lingering in consciousness (Polyn, Norman, & Kahana, 2009; Howard & Kahana, 2002). Together, this information comprises the temporal

context in which a stimulus is encoded. These temporal context representations are thought to gradually drift over time (Figure 2A), changing as stimuli and thoughts enter and fade from consciousness. Critically, these temporal context representations can explain a variety of types of temporal memory decisions and phenomena (DuBrow & Davachi, 2017), including judgments of temporal recency (Howard, Shankar, Aue, & Criss, 2015).

In a study by Howard et al., intracranial electrophysiological signals were recorded as human participants encoded a series of pictures (Howard, Viskontas, Shankar, & Fried, 2012). In particular, they focused on activity patterns in the medial temporal lobe (MTL) given prior evidence implicating MTL regions in encoding contextual information (Jenkins & Ranganath, 2010; Eichenbaum, Yonelinas, & Ranganath, 2007). They found that MTL activity patterns gradually changed over time, consistent with the idea of a slowly drifting temporal context representation. Critically, when a picture repeated (S2), MTL activity patterns jumped back to the state that preceded (and followed) the picture's original occurrence (i.e., activity patterns that were temporally adjacent to S1; Figure 2B). Thus, stimulus repetition putatively triggered the reinstatement of the temporal context in which the stimulus was originally encoded. In a related study, again using intracranial electrophysiological recordings, Manning and colleagues measured neural reinstatement as human participants freely recalled words from a study list (Manning, Polyn, Baltuch, Litt, & Kahana, 2011). They found that when a given stimulus was freely recalled from memory, the evoked neural activity pattern resembled not only the activity pattern evoked by the encoding of that stimulus but also the activity patterns evoked by stimuli that were encoded nearby in time to the recalled stimulus (Figure 2C). Strikingly, this incidental neural reinstatement of temporally adjacent stimuli strongly paralleled the structure of behavioral measures of free recall—namely, after recalling a given word, participants tended to transition to recalling temporally adjacent words (Figure 2C). This provides a critical link between neural measures of temporal context reinstatement and behavioral expressions of the temporal organization of memories.

Although the studies by Howard and colleagues and Manning and colleagues provide compelling and important neural evidence of temporal context reinstatement, it is notable that neither of these studies involved decisions about temporal recency—that is, participants were not asked to recall when events occurred. In a human fMRI study by DuBrow and Davachi, participants studied a series of picture stimuli, with pictures drawn from two different visual categories (faces and objects; DuBrow & Davachi, 2014). During a subsequent temporal recency test, participants were shown pairs of images from the same category (e.g., two faces) and were asked to judge which image occurred most recently (Figure 2D). Pattern classification analyses were used to measure the strength

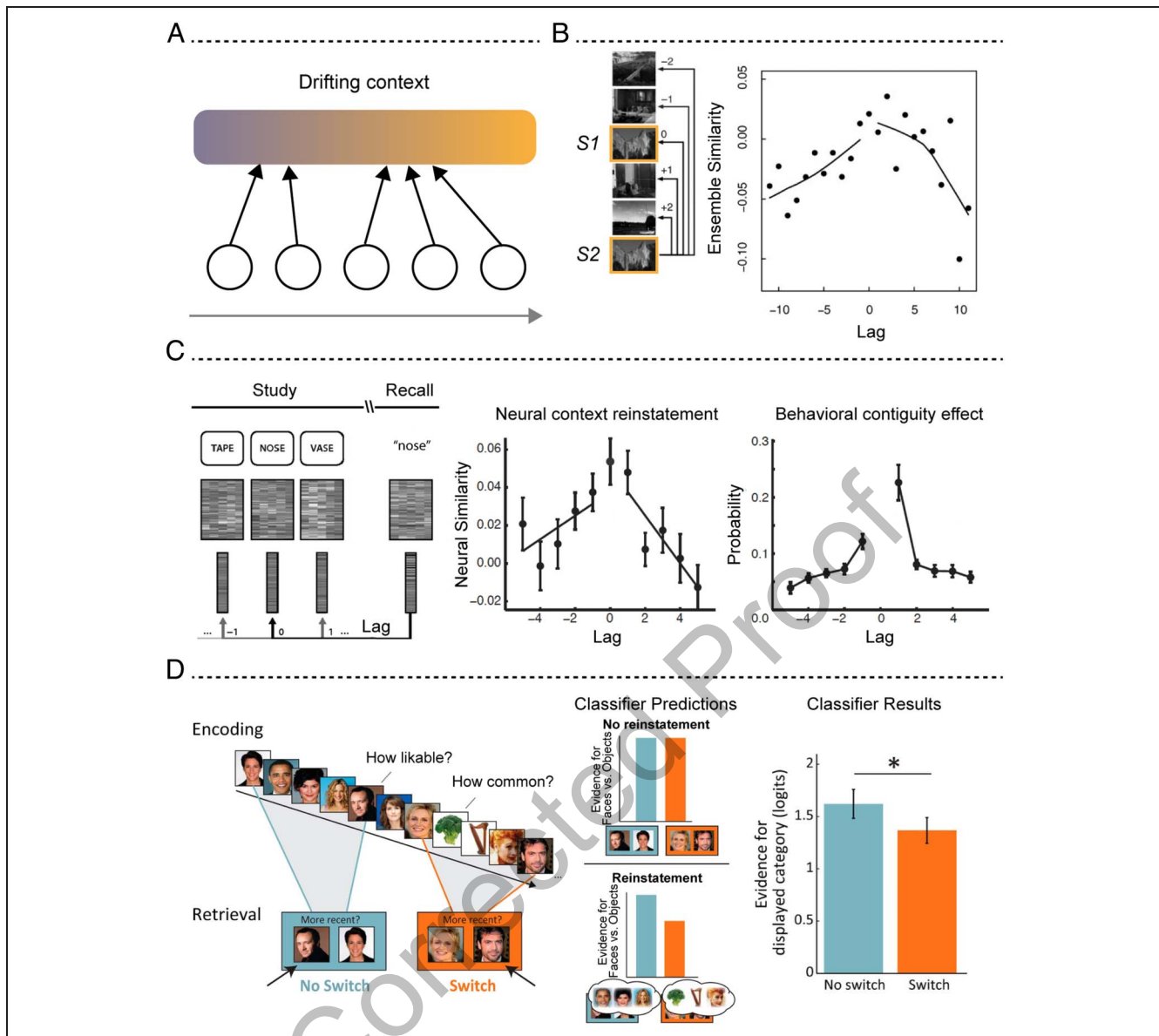


Figure 2. Neural evidence for temporal context reinstatement. (A) According to temporal context models, individual memory traces (circles) are bound to the temporal context in which they occur, which slowly drifts over time (color gradient). (B) Findings from Howard and colleagues (2012) in which participants viewed a series of images while electrophysiological data were recorded. Repetition of a stimulus (S2) triggered reinstatement (ensemble similarity) of the original presentation (S1) and temporally adjacent stimuli. (C) Findings from Manning and colleagues (2011). Participants recalled previously studied words while electrophysiological data were recorded. Neural activity patterns during recall of a word resembled not only the activity pattern during encoding of that word but also the activity patterns during encoding of temporally adjacent words (neural context reinstatement). This neural reinstatement effect paralleled the behavioral tendency to successively recall words that were studied close together in time (behavioral contiguity effect). (D) Findings from DuBrow and Davachi (2014). Human participants encoded images from distinct visual categories (faces vs. objects) and were then shown a pair stimuli and asked to recall which image occurred most recently. If recency judgments involve reinstatement of intervening items, this makes the prediction that when presented with, for example, two faces, neural evidence for faces (measured via pattern classifiers) should be lower if intervening items included objects (Switch condition) versus only faces (No Switch condition). Evidence supported the reinstatement account.

of visual category information (face- or object-related information) during these recency judgments. The key question was whether recency judgments would elicit reinstatement of stimuli that were encoded between the two presented stimuli. Indeed, they found that during temporal memory decisions—where participants were always shown two pictures from the same category—

evidence from the pattern classifiers reflected the categories of images that had intervened during encoding (Figure 2D). In other words, temporally adjacent pictures were reinstated during the recency judgments. DuBrow and Davachi also conducted a parallel behavioral study that further reinforced this conclusion (DuBrow & Davachi, 2014). Collectively, the findings by DuBrow and Davachi provide an

important and direct link between temporal context reinstatement and temporal recency judgments.

Notably, all of the neural evidence for temporal context reinstatement that we describe above comes from situations in which participants were explicitly instructed to recall or to think back to previously encoded information. In other words, these are measures of neural reinstatement during recall. In contrast, we began this article by considering how temporal memories are preserved across repeated encoding of a stimulus. Does neural reinstatement also occur across repeated encoding of a stimulus? This is an important question with respect to ecological relevance because, in the real world, we do not have explicit demands to think back to every prior encounter with a stimulus. Thus, for temporal context reinstatement to be considered a mechanism that protects temporal memories when stimuli repeat, it is imperative to show that stimulus repetitions can trigger neural reinstatement of prior encounters in the absence of explicit demands to recall these prior experiences.

In a series of human fMRI studies, Xue and colleagues measured neural pattern similarity as stimuli were repeatedly encoded (S1, S2, etc.) without any demand to recall prior presentations and, at least in one study, without any knowledge of an upcoming memory test (Xue et al., 2010). They found that greater neural pattern similarity across repetitions was associated with better subsequent recognition memory. They interpreted this finding as evidence that stimulus repetitions triggered—and benefited from—the reinstatement of prior encounters. Although this finding is potentially open to other interpretations that do not involve reinstatement, per se, a reinstatement interpretation is consistent with ideas derived from the behavioral literature reviewed above.

Even stronger evidence that repeated encoding can trigger spontaneous reinstatement comes from studies using classic memory interference paradigms in which a single stimulus is paired with multiple associates (A–B, A–C designs where A represents a repeated stimulus and B and C represent distinct associates). Using pattern-based

fMRI analyses, several studies have shown that A–C encoding trials can elicit spontaneous reinstatement of the B term (i.e., the associate previously encoded with A; Chanales et al., 2019; Koen & Rugg, 2016; Richter, Chanales, & Kuhl, 2016; Zeithamova, Dominick, & Preston, 2012; Kuhl et al., 2010). Although slightly different from evidence of reinstatement of temporally adjacent information, described above, these studies establish the critical point that when a stimulus repeats, even in the absence of explicit demands to recall prior encounters, this can trigger spontaneous reinstatement of prior contextual information. Notably, this spontaneous reinstatement of prior contextual information has also been shown to actively prevent subsequent memory interference (Chanales et al., 2019; Kuhl et al., 2010). However, these examples of neural reinstatement in A–B, A–C paradigms have not been directly connected to subsequent judgments of temporal recency. This represents an important avenue for future research.

Relationship between Repetition-induced Reinstatement and Temporal Memory

Having presented behavioral and neural evidence that repetition of a stimulus can trigger reinstatement of prior encounters with that stimulus, we next turn to the question of “How does repetition-induced reinstatement influence subsequent temporal recency judgments?” Here, there is relatively less evidence to draw from. Moreover, as we note above in our consideration of the existing behavioral evidence, there are multiple viable—and potentially complex—ways in which reinstatement might relate to subsequent temporal recency judgments.

In a recent study (Zou et al., 2023), we tested whether neural pattern similarity across repeated stimulus presentations (S1–S2 similarity) predicted subsequent temporal recency judgments—specifically the amount of time that passed since the stimulus was first encountered (S1 recency; Figure 3A). In this study, the lags between stimulus repetitions ranged from seconds to many months, and

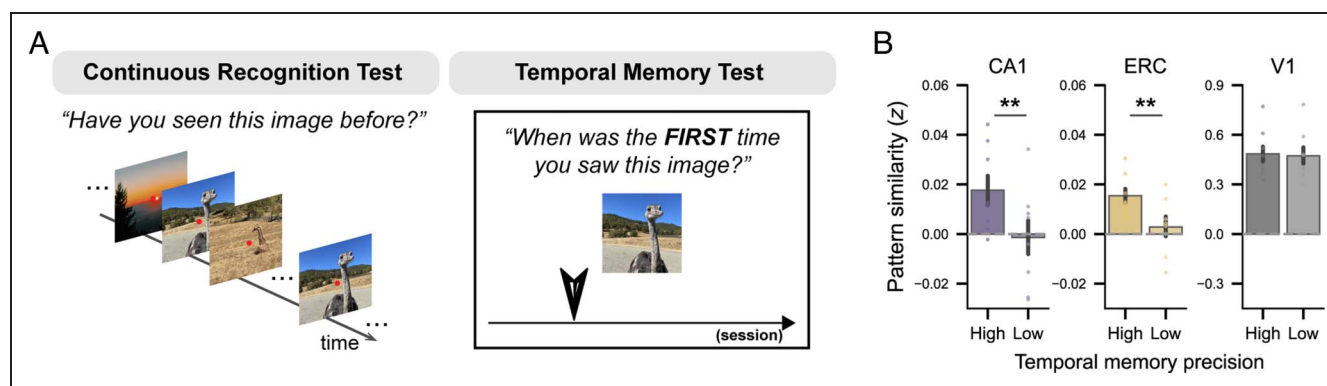


Figure 3. Paradigm and findings from Zou and colleagues (2023). (A) Participants viewed thousands of images distributed, and repeated, across many months. Later, participants performed a temporal recency judgment in which they were asked to estimate when each image was first encountered. (B) Within hippocampal subfield CA1 and entorhinal cortex (ERC), greater neural pattern similarity across stimulus repetitions was associated with more precise temporal memory estimate. This effect was absent in a control region: early visual cortex (V1).

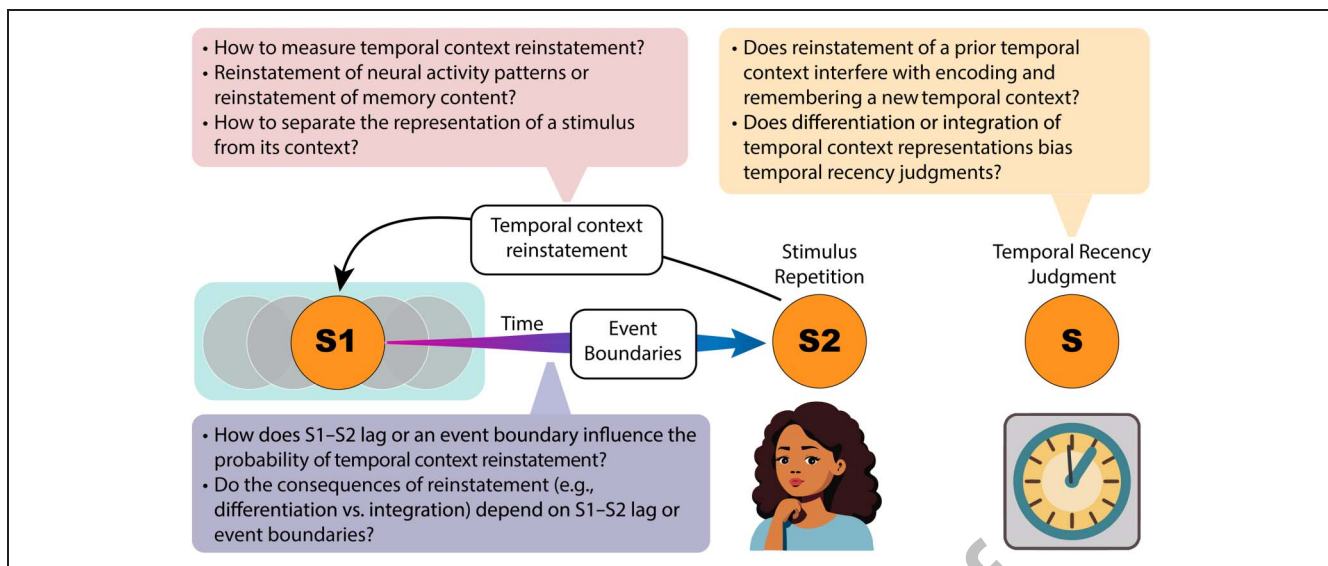


Figure 4. Schematic illustration of relationships between stimulus repetition, temporal context reinstatement, and time/event boundaries. Open questions are presented in text boxes.

temporal recency judgments were only made at the very end of the experiment (after 30–40 experimental sessions distributed across ~10 months). We found that greater neural pattern similarity across stimulus repetitions was associated with better (more precise) temporal recency judgments. Notably, we observed these pattern similarity effects within two MTL subregions that have specifically been implicated in temporal memory (Figure 3B): hippocampal subfield CA1 (Mau et al., 2018; Davachi & DuBrow, 2015; Eichenbaum, 2014; MacDonald, Lepage, Eden, & Eichenbaum, 2011; Huerta, Sun, Wilson, & Tonegawa, 2000) and entorhinal cortex (Montchal, Reagh, & Yassa, 2019; Goyal et al., 2018; Tsao et al., 2018). Although S1–S2 neural pattern similarity is not, as we note above, an unambiguous measure of reinstatement, the fact that these effects occurred within regions implicated in temporal memory is at least consistent with the idea that when encoding a stimulus in a new temporal context (S2), the stimulus’ original temporal context is reinstated and re-encoded, thereby benefiting subsequent judgments of S1 recency. That said, this interpretation would benefit from additional evidence—particularly using methods that more directly measure temporal context reinstatement.

The findings by Zou and colleagues also raise other questions (Figure 4). For example, does reinstatement of the original temporal context (S1) carry potential costs? In particular, it is possible that reinstatement of the S1 context interferes with the encoding of the new temporal context (S2; Duncan, Sadanand, & Davachi, 2012) or that it increases the probability that S2 will be misattributed to S1’s temporal context (Gershman, Schapiro, Hupbach, & Norman, 2013; Sederberg, Gershman, Polyn, & Norman, 2011). In addition, another possibility is that reinstatement might subtly bias temporal memory decisions. In other, nontemporal forms of episodic memory, reinstatement of previously encoded memories that are similar to a

current stimulus has been shown to drive differentiation of corresponding MTL representations (Molitor, Sherrill, Morton, Miller, & Preston, 2021; Chanales, Oza, Favila, & Kuhl, 2017; Kim, Norman, & Turk-Browne, 2017; Favila, Chanales, & Kuhl, 2016; Hulbert & Norman, 2015). Given that representational similarity in the MTL has been directly linked to subjective estimates of elapsed time (Sherman, DuBrow, Winawer, & Davachi, 2023; Lositsky et al., 2016; Ezzyat & Davachi, 2014), an intriguing possibility is that reinstatement-induced differentiation of temporal context representations (in the MTL) results in exaggerated memory for the time between stimulus repetitions—a “repulsive bias.” By this account, reinstatement does not prevent encoding of the S2 temporal context or induce forgetting of the S1 context—rather, each temporal context is remembered relatively accurately, but in a slightly biased manner. As we describe later, temporal memory is prone to subtle biases (Lositsky et al., 2016; Ezzyat & Davachi, 2014; Poynter, 1983), and repulsive biases in memory have been observed for other, nontemporal features (Drascher & Kuhl, 2022; Chanales, Tremblay-McGaw, Drascher, & Kuhl, 2021; Zhao, Chanales, & Kuhl, 2021). Thus, although these ideas are speculative, they represent an interesting avenue for future research.

Repetition Lag and Event Boundaries

In the preceding sections, we advance an argument in which stimulus repetitions induce reinstatement of prior temporal contexts, thereby influencing subsequent judgments of temporal recency. However, as noted in the preceding section, the consequences of reinstatement on temporal memory are not, at present, well understood. Here, we consider a pair of additional factors that may determine the nature of this relationship: (1) the spacing,

or lag, between stimulus repetitions and (2) whether stimulus repetitions span event boundaries.

When a stimulus is repeated after a long lag (high spacing), the probability of retrieving or reinstating the prior encounter with that stimulus will, of course, be diminished (Wixted, 2004). Thus, spacing should influence whether a stimulus repetition induces reinstatement. However, even if reinstatement does occur, spacing may also influence the consequences of reinstatement (Tomparry & Davachi, 2017). In particular, to the extent that temporal context representations drift over time (Manns, Howard, & Eichenbaum, 2007), then the similarity between a reinstated temporal context representation and a current temporal context representation will be inversely proportional to lag. In a recent computational model of spacing effects, Antony and colleagues argue that these two factors—the probability of reinstatement and the degree of similarity between reinstated versus current contexts—can account for key features of spacing effects, including the fact that spacing benefits are non-monotonic (Antony, Liu, Zheng, Ranganath, & O'Reilly, 2023). In their model, as the lag between stimulus repetitions increases, any reinstatement that occurs is more likely to trigger a prediction error signal (owing to greater mismatch between the reinstated and current temporal contexts). Interestingly, they propose that this error signal should lead to abstracted or decontextualized representations. Although the model is not explicitly intended to explain temporal recency effects, it makes an important prediction about the relationship between lag, reinstatement, and temporal memory. Namely, any reinstatement that occurs at long lags should actually disrupt subsequent temporal recency judgments (because of decontextualization). This represents an intriguing prediction that could be empirically tested, but it would require a direct or explicit measure of temporal context reinstatement. Notably, the aforementioned study by Zou and colleagues (Figure 3) found that, in contrast to recognition memory, temporal memory did not benefit from greater spacing (Zou et al., 2023). However, this question would benefit from an experiment explicitly geared toward testing this question.

Importantly, time is not the only way to induce changes in temporal context. Over the past decade, there has been increased interest in the idea that event boundaries can also influence cognitive and neural measures of temporal context (DuBrow, Rouhani, Niv, & Norman, 2017). In contrast to slowly drifting temporal context representations, event boundaries can create discontinuities or shifts in temporal context (DuBrow, 2024; Clewett, DuBrow, & Davachi, 2019; Radvansky & Zacks, 2017). Event boundaries can take many forms, from salient changes in low-level perceptual information (Heusser, Ezzyat, Shiff, & Davachi, 2018) to reward-related prediction errors (Rouhani, Norman, Niv, & Bornstein, 2020). Critically, when two stimuli span an event boundary, they are remembered as occurring farther apart in time (Lositsky et al., 2016; Ezzyat & Davachi,

2014; Poynter, 1983), consistent with the idea that event boundaries induce a change in temporal context, which is then used to infer the elapsed time. Event boundaries have also been shown to powerfully influence temporal order memory—that is, memory for the relative recency of stimuli (Pu, Kong, Ranganath, & Melloni, 2022; Wen & Egner, 2022; Rouhani et al., 2020; Heusser et al., 2018; Horner, Bisby, Wang, Bogus, & Burgess, 2016; DuBrow & Davachi, 2013). In particular, order memory tends to be impaired for stimuli that span an event boundary compared to stimuli within the same event. Thus, event boundaries play a key role in shaping temporal context representations and, thereby, influencing temporal memories.

With respect to the focus of the current article, a key question is whether event boundaries influence the degree to which stimulus repetitions induce reinstatement. That is, does an intervening event boundary between repetitions ($S1 \rightarrow \text{boundary} \rightarrow S2$) increase, decrease, or not affect the probability that $S2$ triggers reinstatement of the $S1$ temporal context? Intuitively, it might be expected that a change in context would reduce the probability that $S2$ would reinstate $S1$. However, at least with respect to recognition memory, there are mixed findings with respect to whether a context change between $S1$ and $S2$ has any influence on the probability of recognition at $S2$ (Baddeley, 1982). Interestingly, boundaries themselves have been shown to trigger reinstatement of preceding stimuli (Sols, DuBrow, Davachi, & Fuentemilla, 2017). Although speculative, it is possible that if a boundary triggers reinstatement of $S1$, this could potentiate additional reinstatement at $S2$. However, to our knowledge, existing studies do not directly test these ideas.

As with changes in temporal context that occur as a function of spacing/lag, changes in temporal context that are driven by event boundaries could also influence the consequences of repetition-induced reinstatement. On the one hand, the difference between the reinstated and current temporal contexts should be greater when repetitions span a boundary (Radvansky & Zacks, 2017), and this could potentially result in error-driven differentiation of the two temporal context representations (Kim et al., 2017). On the other hand, it has been argued that reinstating events that span event boundaries may promote integration across time that prevents differentiation of temporal context representations (Clewett et al., 2019; DuBrow & Davachi, 2016). Thus, building on more general evidence identifying the factors that promote memory differentiation versus integration (Brunec, Robin, Olsen, Moscovitch, & Barense, 2020), it will be of interest to specifically determine how event boundaries influence the consequences of temporal context reinstatement (Figure 4). In particular, an intriguing possibility is that the relative degree of differentiation versus integration induced by reinstatement may be predictive of repulsive versus attractive biases in temporal memory (Bein & Davachi, 2024; DuBrow & Davachi, 2014; Ezzyat & Davachi, 2014).

Summary

The question of how we remember when events occurred in time is a question with a rich history in cognitive psychology (Hintzman, 2003; Friedman, 1993) and neuroscience (Eichenbaum, 2014). The fact that humans are able to form and retain separate temporal memories for experiences that repeat over time is not only important for everyday behavior (e.g., remembering when you last took a medication) but also foundational to theories of episodic memory (Hintzman, 1988). Yet, the mechanisms that protect temporally specific memories in the face of repetition-related interference are not well understood. Here, we propose that repeated encoding of a stimulus can trigger reinstatement of prior temporal contexts in which that stimulus occurred. In turn, this reinstatement may influence subsequent judgments of temporal recency. While we review evidence that this influence can result in the strengthening of the reinstated temporal context, we also raise the possibility that this influence may produce interference or subtle biases in memory.

The idea that stimulus repetitions induce reinstatement of prior experiences is motivated by behavioral studies conducted long before modern neuroscience methods for measuring memory reinstatement (Hintzman et al., 1975; Hintzman & Block, 1973). We believe that more recent neuroimaging and electrophysiological methods for measuring temporal context reinstatement (Yaffe et al., 2014; Howard et al., 2012; Manning et al., 2011; Polyn, Natu, Cohen, & Norman, 2005) create exciting opportunities for revisiting the question of how temporal memories are retained across stimulus repetitions. That said, there is still a need for new methods of measuring temporal context reinstatement that leverage noninvasive neuroimaging techniques and that can more precisely tease apart the representation of a stimulus from its context (Figure 4).

With respect to identifying the specific brain regions that support temporal context reinstatement and behavioral expressions of temporal memory, there is rapidly accumulating—and converging—evidence from human and rodent studies. In particular, hippocampal area CA1 and entorhinal cortex have consistently been implicated in processing and remembering temporal information (Goyal et al., 2018; Mau et al., 2018; Tsao et al., 2018; MacDonald et al., 2011; Huerta et al., 2000), with recent evidence specifically implicating these regions in protecting temporal memories when experiences repeat across time (Zou et al., 2023). Given the many open questions concerning precisely how repetition-induced reinstatement influences temporal memories—including how these dynamics might be influenced by factors such as temporal spacing and event boundaries—additional research related to these topics has the potential to further refine and inform theoretical accounts of temporal context and episodic memory (Davachi & DuBrow, 2015; Howard et al., 2015; Polyn et al., 2009; Howard & Kahana, 2002).

Acknowledgments

This article was inspired by and is dedicated to Dr. Sarah DuBrow. Sarah was a mentor, colleague, and friend of the highest caliber. Her absence looms large, but her influence continues to be felt in so many ways.

Corresponding author: Futing Zou, Department of Psychology, University of Oregon, 1227 University of Oregon, Eugene, OR 97403, or via e-mail: futingz@uoregon.edu.

Author Contributions

Futing Zou: Conceptualization; Visualization; Writing—Original draft; Writing—Review & editing. Brice A. Kuhl: Conceptualization; Funding acquisition; Supervision; Visualization; Writing—Original draft; Writing—Review & editing.

Funding Information

This work was supported by NIH-NINDS (National Institute of Neurological Disorders and Stroke; <https://dx.doi.org/10.13039/100000065>), grant number: R01 NS089729 to B. A. K.

Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were $M(\text{an})/M = .407$, $W(\text{oman})/M = .32$, $M/W = .115$, and $W/W = .159$, the comparable proportions for the articles that these authorship teams cited were $M/M = .549$, $W/M = .257$, $M/W = .109$, and $W/W = .085$ (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

REFERENCES

- Antony, J., 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. *bioRxiv*. <https://doi.org/10.1101/2022.12.01.518703>
- Antony, J. W., Romero, A., Vierra, A. H., Luenser, R. S., Hawkins, R. D., & Bennion, K. A. (2022). Semantic relatedness retroactively boosts memory and promotes memory interdependence across episodes. *eLife*, 11, e72519. <https://doi.org/10.7554/eLife.72519>, PubMed: 35704025
- Baddeley, A. D. (1982). Domains of recollection. *Psychological Review*, 89, 708–729. <https://doi.org/10.1037/0033-295X.89.6.708>
- Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory.

- Neuropsychologia*, 45, 2883–2901. <https://doi.org/10.1016/j.neuropsychologia.2007.06.015>, PubMed: 17675110
- Begg, I., & Green, C. (1988). Repetition and trace interaction: Superadditivity. *Memory & Cognition*, 16, 232–242. <https://doi.org/10.3758/BF03197756>, PubMed: 3393084
- Bein, O., & Davachi, L. (2024). Event integration and temporal differentiation: How hierarchical knowledge emerges in hippocampal subfields through learning. *Journal of Neuroscience*, 44, e0627232023. <https://doi.org/10.1523/JNEUROSCI.0627-23.2023>, PubMed: 38129134
- Brunec, I. K., Robin, J., Olsen, R. K., Moscovitch, M., & Barense, M. D. (2020). Integration and differentiation of hippocampal memory traces. *Neuroscience & Biobehavioral Reviews*, 118, 196–208. <https://doi.org/10.1016/j.neubiorev.2020.07.024>, PubMed: 32712280
- Chanales, A. J. H., Dudukovic, N. M., Richter, F. R., & Kuhl, B. A. (2019). Interference between overlapping memories is predicted by neural states during learning. *Nature Communications*, 10, 5363. <https://doi.org/10.1038/s41467-019-13377-x>, PubMed: 31767880
- Chanales, A. J. H., Oza, A., Favila, S. E., & Kuhl, B. A. (2017). Overlap among spatial memories triggers repulsion of hippocampal representations. *Current Biology*, 27, 2307–2317. <https://doi.org/10.1016/j.cub.2017.06.057>, PubMed: 28736170
- Chanales, A. J. H., Tremblay-McGaw, A. G., Drascher, M. L., & Kuhl, B. A. (2021). Adaptive repulsion of long-term memory representations is triggered by event similarity. *Psychological Science*, 32, 705–720. <https://doi.org/10.1177/0956797620972490>, PubMed: 33882251
- Clewett, D., DuBrow, S., & Davachi, L. (2019). Transcending time in the brain: How event memories are constructed from experience. *Hippocampus*, 29, 162–183. <https://doi.org/10.1002/hipo.23074>, PubMed: 30734391
- Danker, J. F., & Anderson, J. R. (2010). The ghosts of brain states past: Remembering reactivates the brain regions engaged during encoding. *Psychological Bulletin*, 136, 87–102. <https://doi.org/10.1037/a0017937>, PubMed: 20063927
- Davachi, L., & DuBrow, S. (2015). How the hippocampus preserves order: The role of prediction and context. *Trends in Cognitive Sciences*, 19, 92–99. <https://doi.org/10.1016/j.tics.2014.12.004>, PubMed: 25600586
- Drascher, M. L., & Kuhl, B. A. (2022). Long-term memory interference is resolved via repulsion and precision along diagnostic memory dimensions. *Psychonomic Bulletin & Review*, 29, 1898–1912. <https://doi.org/10.3758/s13423-022-02082-4>, PubMed: 35380409
- DuBrow, S. (2024). Event and boundaries. In M. J. Kahana & A. D. Wagner (Eds.), *Oxford handbook of human memory* (Vol. 1). Oxford: Oxford University Press.
- DuBrow, S., & Davachi, L. (2013). The influence of context boundaries on memory for the sequential order of events. *Journal of Experimental Psychology: General*, 142, 1277–1286. <https://doi.org/10.1037/a0034024>, PubMed: 23957281
- DuBrow, S., & Davachi, L. (2014). Temporal memory is shaped by encoding stability and intervening item reactivation. *Journal of Neuroscience*, 34, 13998–14005. <https://doi.org/10.1523/JNEUROSCI.2535-14.2014>, PubMed: 25319696
- DuBrow, S., & Davachi, L. (2016). Temporal binding within and across events. *Neurobiology of Learning and Memory*, 134, 107–114. <https://doi.org/10.1016/j.nlm.2016.07.011>, PubMed: 27422018
- DuBrow, S., & Davachi, L. (2017). Commentary: Distinct neural mechanisms for remembering when an event occurred. *Frontiers in Psychology*, 8, 189. <https://doi.org/10.3389/fpsyg.2017.00189>, PubMed: 28270781
- DuBrow, S., Rouhani, N., Niv, Y., & Norman, K. A. (2017). Does mental context drift or shift? *Current Opinion in Behavioral Sciences*, 17, 141–146. <https://doi.org/10.1016/j.cobeha.2017.08.003>, PubMed: 29335678
- Duncan, K., Sadanand, A., & Davachi, L. (2012). Memory's penumbra: Episodic memory decisions induce lingering mnemonic biases. *Science*, 337, 485–487. <https://doi.org/10.1126/science.1221936>, PubMed: 22837528
- Eichenbaum, H. (2014). Time cells in the hippocampus: A new dimension for mapping memories. *Nature Reviews Neuroscience*, 15, 732–744. <https://doi.org/10.1038/nrn3827>, PubMed: 25269553
- Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, 30, 123–152. <https://doi.org/10.1146/annurev.neuro.30.051606.094328>, PubMed: 17417939
- Ezzyat, Y., & Davachi, L. (2014). Similarity breeds proximity: Pattern similarity within and across contexts is related to later mnemonic judgments of temporal proximity. *Neuron*, 81, 1179–1189. <https://doi.org/10.1016/j.neuron.2014.01.042>, PubMed: 24607235
- Favila, S. E., Chanales, A. J. H., & Kuhl, B. A. (2016). Experience-dependent hippocampal pattern differentiation prevents interference during subsequent learning. *Nature Communications*, 7, 11066. <https://doi.org/10.1038/ncomms11066>, PubMed: 27925613
- Friedman, W. J. (1993). Memory for the time of past events. *Psychological Bulletin*, 113, 44–66. <https://doi.org/10.1037/0033-2909.113.1.44>
- Gershman, S. J., Schapiro, A. C., Hupbach, A., & Norman, K. A. (2013). Neural context reinstatement predicts memory misattribution. *Journal of Neuroscience*, 33, 8590–8595. <https://doi.org/10.1523/JNEUROSCI.0096-13.2013>, PubMed: 23678104
- Goyal, A., Miller, J., Watrous, A. J., Lee, S. A., Coffey, T., Sperling, M. R., et al. (2018). Electrical stimulation in hippocampus and entorhinal cortex impairs spatial and temporal memory. *Journal of Neuroscience*, 38, 4471–4481. <https://doi.org/10.1523/JNEUROSCI.3049-17.2018>, PubMed: 29636396
- 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, 1075–1090. <https://doi.org/10.1037/xlm0000503>, PubMed: 29461067
- Hintzman, D. L. (1988). Judgments of frequency and recognition memory in a multiple-trace memory model. *Psychological Review*, 95, 528–551. <https://doi.org/10.1037/0033-295X.95.4.528>
- Hintzman, D. L. (2003). Judgments of recency and their relation to recognition memory. *Memory & Cognition*, 31, 26–34. <https://doi.org/10.3758/BF03196079>, PubMed: 12699140
- Hintzman, D. L. (2010). How does repetition affect memory? Evidence from judgments of recency. *Memory & Cognition*, 38, 102–115. <https://doi.org/10.3758/MC.38.1.102>, PubMed: 19966243
- Hintzman, D. L., & Block, R. A. (1973). Memory for the spacing of repetitions. *Journal of Experimental Psychology*, 99, 70–74. <https://doi.org/10.1037/h0034761>
- Hintzman, D. L., Summers, J. J., & Block, R. A. (1975). Spacing judgments as an index of study-phase retrieval. *Journal of Experimental Psychology: Human Learning and Memory*, 1, 31–40. <https://doi.org/10.1037/0278-7393.1.1.31>
- 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. <https://doi.org/10.1016/j.cognition.2016.05.013>, PubMed: 27295330

- Howard, M. W., & Kahana, M. J. (2002). A distributed representation of temporal context. *Journal of Mathematical Psychology*, *46*, 269–299. <https://doi.org/10.1006/jmps.2001.1388>
- Howard, M. W., Shankar, K. H., Aue, W. R., & Criss, A. H. (2015). A distributed representation of internal time. *Psychological Review*, *122*, 24–53. <https://doi.org/10.1037/a0037840>
- Howard, M. W., Viskontas, I. V., Shankar, K. H., & Fried, I. (2012). Ensembles of human MTL neurons “jump back in time” in response to a repeated stimulus. *Hippocampus*, *22*, 1833–1847. <https://doi.org/10.1002/hipo.22018>, PubMed: 22488671
- Huerta, P. T., Sun, L. D., Wilson, M. A., & Tonegawa, S. (2000). Formation of temporal memory requires NMDA receptors within CA1 pyramidal neurons. *Neuron*, *25*, 473–480. [https://doi.org/10.1016/S0896-6273\(00\)80909-5](https://doi.org/10.1016/S0896-6273(00)80909-5), PubMed: 10719900
- Hulbert, J. C., & Norman, K. A. (2015). Neural differentiation tracks improved recall of competing memories following interleaved study and retrieval practice. *Cerebral Cortex*, *25*, 3994–4008. <https://doi.org/10.1093/cercor/bhu284>, PubMed: 25477369
- Jacoby, L. L., & Wahlheim, C. N. (2013). On the importance of looking back: The role of recursive reminders in recency judgments and cued recall. *Memory & Cognition*, *41*, 625–637. <https://doi.org/10.3758/s13421-013-0298-5>, PubMed: 23371792
- Jenkins, L. J., & Ranganath, C. (2010). Prefrontal and medial temporal lobe activity at encoding predicts temporal context memory. *Journal of Neuroscience*, *30*, 15558–15565. <https://doi.org/10.1523/JNEUROSCI.1337-10.2010>, PubMed: 21084610
- Kim, G., Norman, K. A., & Turk-Browne, N. B. (2017). Neural differentiation of incorrectly predicted memories. *Journal of Neuroscience*, *37*, 2022–2031. <https://doi.org/10.1523/JNEUROSCI.3272-16.2017>, PubMed: 28115478
- Koen, J. D., & Rugg, M. D. (2016). Memory reactivation predicts resistance to retroactive interference: Evidence from multivariate classification and pattern similarity analyses. *Journal of Neuroscience*, *36*, 4389–4399. <https://doi.org/10.1523/JNEUROSCI.4099-15.2016>, PubMed: 27076433
- Kuhl, B. A., Shah, A. T., DuBrow, S., & Wagner, A. D. (2010). Resistance to forgetting associated with hippocampus-mediated reactivation during new learning. *Nature Neuroscience*, *13*, 501–506. <https://doi.org/10.1038/nn.2498>, PubMed: 20190745
- Lositsky, O., Chen, J., Toker, D., Honey, C. J., Shvartsman, M., Poppenk, J. L., et al. (2016). Neural pattern change during encoding of a narrative predicts retrospective duration estimates. *eLife*, *5*, e16070. <https://doi.org/10.7554/eLife.16070>, PubMed: 27801645
- MacDonald, C. J., Lepage, K. Q., Eden, U. T., & Eichenbaum, H. (2011). Hippocampal “time cells” bridge the gap in memory for discontinuous events. *Neuron*, *71*, 737–749. <https://doi.org/10.1016/j.neuron.2011.07.012>, PubMed: 21867888
- Manning, J. R., Polyn, S. M., Baltuch, G. H., Litt, B., & Kahana, M. J. (2011). Oscillatory patterns in temporal lobe reveal context reinstatement during memory search. *Proceedings of the National Academy of Sciences, U.S.A.*, *108*, 12893–12897. <https://doi.org/10.1073/pnas.1015174108>, PubMed: 21737744
- Manns, J. R., Galloway, C. R., & Sederberg, P. B. (2015). A temporal context repetition effect in rats during a novel object recognition memory task. *Animal Cognition*, *18*, 1031–1037. <https://doi.org/10.1007/s10071-015-0871-3>, PubMed: 25917312
- Manns, J. R., Howard, M. W., & Eichenbaum, H. (2007). Gradual changes in hippocampal activity support remembering the order of events. *Neuron*, *56*, 530–540. <https://doi.org/10.1016/j.neuron.2007.08.017>, PubMed: 17988635
- 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*, *28*, 1499–1508. <https://doi.org/10.1016/j.cub.2018.03.051>, PubMed: 29706516
- Mensink, G.-J., & Raaijmakers, J. G. (1988). A model for interference and forgetting. *Psychological Review*, *95*, 434–455. <https://doi.org/10.1037/0033-295X.95.4.434>
- Molitor, R. J., Sherrill, K. R., Morton, N. W., Miller, A. A., & Preston, A. R. (2021). Memory reactivation during learning simultaneously promotes dentate gyrus/CA_{2,3} pattern differentiation and CA₁ memory integration. *Journal of Neuroscience*, *41*, 726–738. <https://doi.org/10.1523/JNEUROSCI.0394-20.2020>, PubMed: 33239402
- Montchal, M. E., Reagh, Z. M., & Yassa, M. A. (2019). Precise temporal memories are supported by the lateral entorhinal cortex in humans. *Nature Neuroscience*, *22*, 284–288. <https://doi.org/10.1038/s41593-018-0303-1>, PubMed: 30643291
- Morton, J. (1968). Repeated items and decay in memory. *Psychonomic Science*, *10*, 219–220. <https://doi.org/10.3758/BF03331489>
- Polyn, S. M., Natu, V. S., Cohen, J. D., & Norman, K. A. (2005). Category-specific cortical activity precedes retrieval during memory search. *Science*, *310*, 1963–1966. <https://doi.org/10.1126/science.1117645>, PubMed: 16373577
- 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. <https://doi.org/10.1037/a0014420>, PubMed: 19159151
- Poynter, W. D. (1983). Duration judgment and the segmentation of experience. *Memory & Cognition*, *11*, 77–82. <https://doi.org/10.3758/BF03197664>, PubMed: 6855562
- Pu, Y., Kong, X.-Z., Ranganath, C., & Melloni, L. (2022). Event boundaries shape temporal organization of memory by resetting temporal context. *Nature Communications*, *13*, 622. <https://doi.org/10.1038/s41467-022-28216-9>, PubMed: 35110527
- Radvansky, G. A., & Zacks, J. M. (2017). Event boundaries in memory and cognition. *Current Opinion in Behavioral Sciences*, *17*, 133–140. <https://doi.org/10.1016/j.cobeha.2017.08.006>, PubMed: 29270446
- Richter, F. R., Chanals, A. J. H., & Kuhl, B. A. (2016). Predicting the integration of overlapping memories by decoding mnemonic processing states during learning. *Neuroimage*, *124*, 323–335. <https://doi.org/10.1016/j.neuroimage.2015.08.051>, PubMed: 26327243
- Rouhani, N., Norman, K. A., Niv, Y., & Bornstein, A. M. (2020). Reward prediction errors create event boundaries in memory. *Cognition*, *203*, 104269. <https://doi.org/10.1016/j.cognition.2020.104269>, PubMed: 32563083
- Sederberg, P. B., Gershman, S. J., Polyn, S. M., & Norman, K. A. (2011). Human memory reconsolidation can be explained using the temporal context model. *Psychonomic Bulletin & Review*, *18*, 455–468. <https://doi.org/10.3758/s13423-011-0086-9>, PubMed: 21512839
- Sherman, B. E., DuBrow, S., Winawer, J., & Davachi, L. (2023). Mnemonic content and hippocampal patterns shape judgments of time. *Psychological Science*, *34*, 221–237. <https://doi.org/10.1177/09567976221129533>, PubMed: 36442582
- Siegel, L. L., & Kahana, M. J. (2014). A retrieved context account of spacing and repetition effects in free recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *40*, 755–764. <https://doi.org/10.1037/a0035585>, PubMed: 24564545

- 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*, *27*, 3499–3504. <https://doi.org/10.1016/j.cub.2017.09.057>, PubMed: 29129536
- Tomparry, A., & Davachi, L. (2017). Consolidation promotes the emergence of representational overlap in the hippocampus and medial prefrontal cortex. *Neuron*, *96*, 228–241. <https://doi.org/10.1016/j.neuron.2017.09.005>, PubMed: 28957671
- Tsao, A., Sugar, J., Lu, L., Wang, C., Knierim, J. J., Moser, M.-B., et al. (2018). Integrating time from experience in the lateral entorhinal cortex. *Nature*, *561*, 57–62. <https://doi.org/10.1038/s41586-018-0459-6>, PubMed: 30158699
- Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, *53*, 1–25. <https://doi.org/10.1146/annurev.psych.53.100901.135114>, PubMed: 11752477
- Wen, T., & Egner, T. (2022). Retrieval context determines whether event boundaries impair or enhance temporal order memory. *Cognition*, *225*, 105145. <https://doi.org/10.1016/j.cognition.2022.105145>, PubMed: 35483158
- Wixted, J. T. (2004). The psychology and neuroscience of forgetting. *Annual Review of Psychology*, *55*, 235–269. <https://doi.org/10.1146/annurev.psych.55.090902.141555>, PubMed: 14744216
- Xue, G., Dong, Q., Chen, C., Lu, Z., Mumford, J. A., & Poldrack, R. A. (2010). Greater neural pattern similarity across repetitions is associated with better memory. *Science*, *330*, 97–101. <https://doi.org/10.1126/science.1193125>, PubMed: 20829453
- Yaffe, R. B., Kerr, M. S. D., Damera, S., Sarma, S. V., Inati, S. K., & Zaghoul, K. A. (2014). Reinstatement of distributed cortical oscillations occurs with precise spatiotemporal dynamics during successful memory retrieval. *Proceedings of the National Academy of Sciences, U.S.A.*, *111*, 18727–18732. <https://doi.org/10.1073/pnas.1417017112>, PubMed: 25512550
- Yntema, D. B., & Trask, F. P. (1963). Recall as a search process. *Journal of Verbal Learning and Verbal Behavior*, *2*, 65–74. [https://doi.org/10.1016/S0022-5371\(63\)80069-9](https://doi.org/10.1016/S0022-5371(63)80069-9)
- Yonelinas, A. P., Ranganath, C., Ekstrom, A. D., & Wiltgen, B. J. (2019). A contextual binding theory of episodic memory: Systems consolidation reconsidered. *Nature Reviews Neuroscience*, *20*, 364–375. <https://doi.org/10.1038/s41583-019-0150-4>, PubMed: 30872808
- Zeithamova, D., Dominick, A. L., & Preston, A. R. (2012). Hippocampal and ventral medial prefrontal activation during retrieval-mediated learning supports novel inference. *Neuron*, *75*, 168–179. <https://doi.org/10.1016/j.neuron.2012.05.010>, PubMed: 22794270
- Zhao, Y., Chanals, A. J. H., & Kuhl, B. A. (2021). Adaptive memory distortions are predicted by feature representations in parietal cortex. *Journal of Neuroscience*, *41*, 3014–3024. <https://doi.org/10.1523/JNEUROSCI.2875-20.2021>, PubMed: 33619210
- Zou, F., Wanjia, G., Allen, E. J., Wu, Y., Charest, I., Naselaris, T., et al. (2023). Re-expression of CA1 and entorhinal activity patterns preserves temporal context memory at long timescales. *Nature Communications*, *14*, 4350. <https://doi.org/10.1038/s41467-023-40100-8>, PubMed: 37468489

Corrected Proof