Context Change Shapes the Organization of Memory Recall

by

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DISSERTATION ABSTRACT

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Our memories of past experiences are strongly linked to rich contextual details—that is, memory for where or when an event took place. This contextual information not only supports memory retrieval but also shapes how memories are organized. Free recall tasks provide a unique window into these organizational processes, revealing that memory organization is often guided by the similarity of contextual features during learning. Contexts can be similar along a number of dimensions, including temporal, source, and motivational context. However, the context in which we form memories is constantly changing, and while context is known to support memory, it remains unclear how such changes influence what is remembered and how memories are organized.

Across three studies, this dissertation explores how features of context change influence the organization of free recall memory, using both behavioral measures and brain activity measured with functional magnetic resonance imaging (fMRI). **Chapter II** presents two behavioral studies using a context switching paradigm to examine how the frequency and relative novelty of context changes interact to influence free recall. I found that recall performance is worse only when rapidly switching to novel contexts. This suggests not only a benefit for switching to a familiar context, but that impairments of switching to novel environments only emerged in the context of rapid versus slower switches. This difference may have been due, in part, to differences in memory organization. **Chapter III** is an fMRI study in which the rate of external context change was manipulated during encoding. I tested whether this affected memory organization, measured using

temporal clustering—the tendency to recall items in the order they were studied. I also examined whether these behavioral patterns were mirrored in the brain by looking at gradually changing activity in the hippocampus. A higher rate of context change was associated with both less temporal clustering and lower hippocampal autocorrelation, a measure of the stability of hippocampal activity patterns over time. Moreover, participants who exhibited greater hippocampal autocorrelation during encoding also exhibited stronger temporal clustering during recall, establishing a link between hippocampal autocorrelation and temporal organization of memory. **Chapter IV** used a between-subjects free recall paradigm to test whether agency—having control over one's choices—can act as a context to organize memories. I found that participants with agency showed reduced temporal clustering compared to yoked participants who had no choice. Instead, participants with agency organized their memories more around the meaningful connections they constructed through their choices. Collectively, these findings provide novel insight into how contextual factors shape the organization of memory.

This dissertation includes previously published and unpublished co-authored material.

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CHAPTER I

INTRODUCTION

Memories are not stored in isolation; they are embedded within the context in which they were formed. What we remember is deeply shaped by the places we visit, how long we were there, and the events unfolding around us. These contextual details help anchor our memories, allowing us to mentally re-experience past events—such as vividly recalling the setting of a meaningful conversation or the atmosphere of a significant life event. The ability to retrieve specific experiences, complete with the contextual details that define them, is known as episodic memory (Tulving, 2002). Context not only supports memory retrieval but also shapes how memories are structured and organized over time.

One way to examine how context influences memory is through free recall, a task in which individuals remember studied information without external cues. This method allows researchers to investigate not only how much information is remembered but also the order in which it is recalled—that is, how memories are organized. Studies of free recall have demonstrated that the order in which items are recalled from memory is influenced by the similarity of the contexts in which they were encoded (Howard & Kahana, 2002; Polyn et al., 2009a; Sederberg et al., 2008). This is evidenced by recall transitions—where it is more likely that individuals will recall two items in immediate succession that share a similar context. In this way, the organization of items in free recall is thought to provide a window into the structure of natural memories and the underlying contextual representations.

However, our environment is constantly changing. As we move through different locations, engage with different people, or shift between tasks, the context in which memories are formed evolves. These features of our environment may change abruptly or shift gradually over time

(DuBrow et al., 2017; Polyn et al., 2009a). These fluctuations in context play a crucial role in shaping both how much we remember and how our memories are organized. For example, imagine attending a conference where you listen to multiple talks throughout the day. If you were asked to recall which talks you went to, you might recall the talks in the order they happened, remembering first what you heard in the morning before lunch and then what you heard in the afternoon. Alternatively, your memory could be structured by topic—you might group together all the talks related to episodic memory, even if they were spread throughout the day, and separately recall those about decision-making. Prior research has shown that sudden context changes—such as changes in perceptual attributes (Heusser et al., 2018), task set (Polyn et al., 2009b), and stimulus class (DuBrow & Davachi, 2013, 2016)—can shape how information is remembered. However, it remains unclear how different features of context change influence the organization of free recall memory.

One key aspect of context change that may influence memory organization is its switch rate. Slower changes in context have been shown to provide structure for memory (Polyn et al., 2009b), but the effects of more rapid context changes remain unknown. These effects may also depend on an individual's familiarity with the environment—while distinct or novel events can serve as meaningful boundaries that support memory, too much novelty or frequent disruptions may impair recall. Beyond external context shifts, internal factors also shape how memories are organized during free recall (Wang et al., 2023). For instance, having agency over a decision influences subsequent temporal memory judgments (Houser et al., 2022), yet little is known about whether actively making a choice between contexts affects memory organization. Clarifying how these factors interact is essential for uncovering the mechanisms underlying memory organization.

While the link between context processing and recall has been well studied across a diverse range of behavioral studies, a growing number of studies additionally provide insight into the underlying neural mechanisms at play. Specifically, the hippocampus is thought to be a key structure involved in both context processing and our ability to recall the past (Baldassano et al., 2017; Ben-Yakov & Dudai, 2011; DuBrow & Davachi, 2016). Famously, the case study of Patient H.M., who had damage to his hippocampus and other nearby structures, revealed that he was unable to form or subsequently recall any new episodic memories following his injury (Scoville & Milner, 1957). More recently, a number of studies across modalities and species have also implicated the hippocampus in various aspects of context processing (see Davachi, 2006; Eichenbaum et al., 2007, 2012; Maren et al., 2013; Ranganath, 2010a, 2010b; Ross & Easton, 2021; Rudy, 2009; Smith & Mizumori, 2006 for reviews). Taken together, these lines of literature strongly suggest that the hippocampus plays a fundamental role in linking contextual information to how and what we recall.

The aim of this dissertation is to better understand how changes in context during encoding influence free recall memory. The work in this dissertation describes a series of experiments that use novel behavioral paradigms to examine how memories are shaped by contextual information, alongside advanced functional magnetic resonance imaging (fMRI) techniques. Specifically, this dissertation investigates: 1) how qualitative features of context change influence memory structure and organization, 2) whether hippocampal context representations are linked to temporal memory organization during free recall, and 3) whether having agency serves as a context for structuring memories. The remaining sections of this chapter will review relevant background before moving on to detailed descriptions of each study in the subsequent chapters.

Context change shapes free recall

Context change influences overall recall performance

Context plays a critical role in both remembering and forgetting, with changes in context shaping how much information is later recalled. For instance, research using both the segmentation of continuous events (Flores et al., 2017; Schwan et al., 2000) and shifts in experimental context (Pettijohn et al., 2016; Smith et al., 1978) found that memory performance is often enhanced when an experience includes a meaningful context change. This overall recall benefit is especially pronounced when the task requires participants to actively attend to the meaningful change points in an event (Boltz, 1992; Gold et al., 2017; Schwan et al., 2000; Schwan & Garsoffky, 2004). However, while context changes can enhance memory for new information, they may also come at a cost. Findings from context-dependent memory literature indicate that recall is often impaired when the context at study does not match the context at retrieval (Godden & Baddeley, 1975; Sahakyan & Kelley, 2002; Shin et al., 2021; Smith et al., 1978; Smith & Vela, 2001; Unsworth et al., 2012). Taken together, these findings suggest that the effects of context changes on memory depend on specific features of the change itself. It remains unclear what determines whether a change in context enhances or disrupts recall memory.

One key feature that may shape the effects of context on memory is the rate of context change. In the real world, different situations are often accompanied by dramatically different numbers of contexts. For instance, a postal worker can spend their whole day delivering packages to multiple different houses or alternatively, to just a few large apartment building mailrooms. Studies suggest that learning across multiple contexts can reduce the impairment typically seen when memory is tested in a novel context (Smith, 1982). For example, recall performance improves when word lists are studied in multiple spatial locations (two, three, or four) rather than in a single setting (Smith, 1982; Smith, 1984; Smith et al., 1978; Smith & Rothkopf, 1984). Similarly, one study found that in narratives with event shifts, stories with two shifts enhanced overall recall performance compared with those with only one shift (Pettijohn et al., 2016). However, it remains unclear whether increasing the rate of context changes continues to benefit recall or if there is a point at which too many shifts become disruptive.

According to contextual variability theory, items will be more easily recalled if they are tagged with more varied contexts, as each distinct context provides additional paths to retrieve the item (Lohnas et al., 2011). Even if an item is only encountered once, our internal context is thought to drift slowly, so items may be tagged with the current as well as the previous external context. As depicted in Figure 1.1, when slowly alternating between two different tasks the internal context that tags individual items is highly differentiated (i.e., tends to be either red or blue). When trying to remember those items, recall may be limited by only having a single contextual cue for retrieval. By contrast, when more rapidly switching, it is possible that part of the prior context not only lingers into the next context, but also overlaps, creating a "blended" contextual representation, such that individual items are tagged with both contextual cues (depicted in purple; Polyn et al., 2012). This could be helpful for memory in that items now have more contextual cues for retrieval (Lohnas et al., 2011; Siegel & Kahana, 2014). However, it could also be harmful for memory due to heightened interference and competition (Anderson, 2003), or decreased novelty typically associated with a context switch (Polyn et al., 2012). The effects of the rate of context change on memory performance may also interact with other factors, such as the individual's familiarity with the contexts.

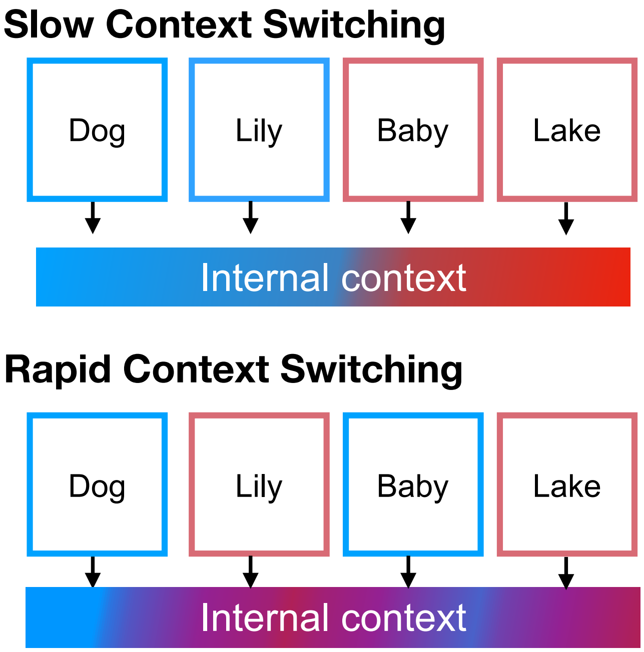

Figure 1.1 Schematic depicting internal context representations based on the rate of external context changes (slow vs. rapid). Colors represent different tasks or categories. Outline represents external context and gradient bars represent internal context.

Context change and memory for boundary information

Context changes can also prioritize the encoding of information at the change point, or event boundary. In one task-switching study, participants were more likely to recall the boundary item first in the recall sequence, and there was a recall advantage for items studied immediately after the context shift (Polyn et al., 2009b). A similar boundary enhancement was observed using naturalistic navigation (Jeunehomme & D'Argembeau, 2020). These findings are consistent with the idea that event boundaries trigger increased attention to salient, new information, which in turn is associated with better memory for information encountered at the boundary (Clewett et al., 2019; Zacks & Swallow, 2007). However, some studies found no consistent boost in free recall for boundary items (Heusser et al., 2018; Pettijohn et al., 2016). Additionally, one study even reported both a benefit and a lack of a clear advantage in recalling boundary items within the same paradigm. In this movie viewing study, explicitly cueing boundaries through editing led to higher recall for those segments compared with unedited clips (which had the same boundaries), suggesting that directing attention to boundaries may be essential for memory benefits (Gold et al., 2017). Determining the specific conditions under which recall memory for boundary information is enhanced is an important avenue for future research.

Context change restructures memory organization

According to computational models of free recall, memory search is thought to be guided by internally maintained representations of context. This context representation contains information related to temporal context, source information, and semantic characteristics (Polyn et al., 2009a). An item's temporal context consists of recently studied items, other environmental cues, as well as the individuals' internal thoughts and emotions. This temporal context representation has been thought to drift slowly over time (Howard & Kahana, 2002; Polyn et al., 2009a). When two temporally adjacent items are studied within the same slowly drifting context, an indirect association forms between them, linking them over time (DuBrow et al., 2017). During recall, the current context serves as a retrieval cue, activating memories of items encoded in similar contextual states. With each recalled item, the context updates, influencing the order of subsequently recalled items. This explains the well-established phenomenon of temporal clustering, where individuals tend to recall items in the order in which they were originally studied (Kahana, 1996; Sederberg et al., 2010). Temporal clustering has been previously thought to be very durable, surviving the insertion of a distractor task before every item (Howard & Kahana, 1999). While prior studies have since shown that temporal clustering can be influenced by manipulating features of the stimuli themselves (Hong et al., 2024; Manning et al., 2023), future work is needed to determine how changing the external context influences temporal clustering.

Source context reflects the content of the information present at encoding beyond the gradually drifting temporal representation. This includes features such as the type of stimulus used or the task participants are instructed to perform (DuBrow & Davachi, 2013; Murdock & Walker, 1969; Polyn et al., 2009a, 2009b). A sudden shift in the external environment, task, or internally maintained goals can lead to a disruption or reorganization of the source context representation. Although free recall is inherently unconstrained–allowing participants to recall items in any order–substantial evidence suggests that salient environmental changes impose structure on memory by isolating items studied before and after a context change. Specifically, items encountered within the same context are more likely to be recalled together, a phenomenon known as source clustering (Hintzman et al., 1972; Murdock & Walker, 1969; Polyn et al., 2009a, 2009b, 2012; Smith, 1982). Moreover, research indicates that participants are more likely to transition between successive recalls within the same context rather than across contexts (Chan et al., 2017; Heusser et al., 2018; Lohnas et al., 2023; Polyn et al., 2009b). This suggest that while context changes can facilitate the organization of memories by grouping related information together (e.g., recalling items studied with the same task together), they can also make it more difficult to retrieve information across contexts. How temporal and source context interact when contexts change is still unclear.

Motivational states as a context for memory organization

The studies discussed so far have focused on how memories are organized for neutral information. However, many studies have explored motivational state as a source context (Rouhani et al., 2020; Talmi et al., 2021; Wang et al., 2023). While much of this work examines how motivation influences memory performance, several studies have also shown that motivational states structure memory organization. For instance, one study had participants study positive, neutral, and negative words in a free recall task. Participants were significantly more likely to recall successive words of the same valence (e.g., positive to positive) than words of different valence (e.g., positive to negative; Long et al., 2015). This effect has been extended to reward motivation, where participants learned lists of words that were associated with high or low rewards (Horwath et al., 2023). Similarly, participants were more likely to transition between words of the same reward category, but this effect was specific to highly rewarded items, suggesting that reward served as an organizational category for valuable items (Horwath et al., 2023). In contrast, a study examining motivation through threat vs. instruction-based incentives found that threat impaired the organization of memory around motivation value compared to instructed motivation (Horwath et al., 2024). Notably, in the both studies, temporal clustering did not differ across motivation conditions (Horwath et al., 2023, 2024). Together these findings suggest that recalling items in temporal order is not always adaptive. Instead, motivational states may serve as a context to organize memories, though this organization appears disrupted with threat. However, it remains unknown whether these effects persist when individuals have agency over their choices.

The hippocampus and context memory

Hippocampal involvement in context processing

Episodic memory involves forming associations between individual events and the context in which they occurred. The hippocampus is thought to play a critical role in this process, as evidenced by research in humans (Chun & Phelps, 1999; Herz et al., 2023; Long et al., 2017; Miller et al., 2013) and rodents (Corcoran & Maren, 2001; Komorowski et al., 2009, 2013;

McKenzie et al., 2014). For instance, in a visual search task, amnesic patients with hippocampal damage showed normal improvements in general search speed. However, unlike healthy individuals, they did not exhibit any context-dependent learning—where repeated exposure to the same displays would typically help locate the target more quickly over time (Chun & Phelps, 1999). Additionally, contextual factors have also been shown to directly influence hippocampal activity (Baldassano et al., 2017; Dimsdale-Zucker et al., 2018; DuBrow & Davachi, 2014, 2016; Geva-Sagiv et al., 2023). In one line of work, researchers found that the offset of movie clips was related to increased hippocampal activity, which correlated with later memory (Ben-Yakov et al., 2013; Ben-Yakov & Dudai, 2011). Further research is needed to examine how changes in context influence activity in the hippocampus.

Hippocampal drift

Much of our internal temporal context representations drift more slowly than our changing external environment (DuBrow et al., 2017; Polyn et al., 2009a). This slowly drifting temporal context representation has been thought to be reflected in gradually changing patterns of activity in the hippocampus. For instance, evidence in both humans (Folkerts et al., 2018) and rodents (Manns et al., 2007) suggests that hippocampal activity patterns become more dissimilar as the temporal distance between experiences increases. Additionally, hippocampal time cells gradually change their activity patterns over seconds during moments of empty periods in a sequence (Eichenbaum, 2014; MacDonald et al., 2011; Umbach et al., 2020), reinforcing the idea that the hippocampus maintains a continuous representation of temporal context. If the hippocampus is continuously tracking changes in context, how might this be reflected in behavior?

Several lines of evidence support the idea that this hippocampal drift is relevant to episodic memory. For example, the degree of drift in the hippocampus during the encoding of a sequence of stimuli is predictive of subsequent temporal memory judgments for those stimuli (DuBrow & Davachi, 2014; Ezzyat & Davachi, 2014; Jenkins & Ranganath, 2016; Manns et al., 2007). More recently, researchers have used autocorrelation analyses to quantify how hippocampal activity changes slowly over time (Bouffard et al., 2023; Brunec et al., 2018; Coughlan et al., 2023). These researchers found that hippocampal drift is modulated by navigation behavior (Bouffard et al., 2023; Brunec et al., 2018), such that as navigation difficulty increases, the amount of drift decreases, as reflected by increased autocorrelation. Yet, there is a surprising lack of evidence directly linking hippocampal drift rate to behavior, specifically in free recall.

Overview of the present work

The goals of this dissertation are to: 1) examine how specific features of context change shape recall performance and organization and 2) test whether memory organization relates to drifting context representations in the hippocampus. In three empirical studies, I will show that manipulations of external (**Chapters II and III**) and internal context (**Chapter IV**) influence the rate of internal contextual drift specifically in the hippocampus (**Chapter III only**), and influence how free recall memory is organized. Importantly, these chapters will demonstrate that different features of context change will lead to different ways to organize memory. Together, these studies add to a growing literature characterizing the effects of context on episodic memory and further our understanding of the role of the hippocampus in free recall memory.

In **Chapter II**, I test how the interaction between the rate of context change and an individual's familiarity with the context influences free recall memory. I found and replicated that free recall memory was only impaired when switching quickly between novel contexts, not when switching quickly between familiar contexts. In fact, when the context was familiar, memory was just as good when the context was changing rapidly vs. when it was not changing at all. Lastly, using clustering analyses, we observed that the order in which participants recalled the items differed when the context switched rapidly depending on whether the contexts were familiar or novel.

In **Chapter III**, I test whether there is a direct link between temporal clustering in recall and drifting contextual representations in the hippocampus during encoding. While context switch rate had no effect on the total number of words recalled, I found that it significantly influenced the degree of temporal clustering. Specifically, a higher context switch rate was associated with less temporal clustering. Using autocorrelation analyses to measure hippocampal drift (Bouffard et al., 2023; Brunec et al., 2018), we found that this pattern of data was mirrored by autocorrelation in the hippocampus: autocorrelation significantly decreased when switch rate increased. Most importantly, I found that hippocampal autocorrelation during encoding was positively correlated with temporal clustering during free recall.

In **Chapter IV**, I test whether imbuing participants with agency over a decision can act as a context to organize memories. I found that participants with agency showed reduced temporal clustering compared to participants who had no control over their choices, suggesting that recalling items in strict temporal order may not always be the most adaptive strategy. Instead, I found that having agency over a choice led participants to organize their memories more around the relationships they actively constructed through their choices. Finally, **Chapter V** will summarize the presented empirical findings and provide a general discussion that ties them to the broader literature.

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CHAPTER II

CONTEXTUAL FAMILIARITY RESCUES THE COST OF SWITCHING

From Rait, L. I., Murty, V. P., & DuBrow, S. (2024). Contextual familiarity rescues the cost of switching. Psychonomic Bulletin & Review, 31(3), 1103-1113.

Introduction

Our environment is ever-changing, filled with switches in context varying in how often switches occur as well as prior exposure to the contexts (i.e., relative novelty). These types of changes profoundly influence how we form and structure memories. For instance, imagine watching a movie in the living room while preparing dinner in the kitchen. If asked to recall what happened in the movie, your later memory of a specific scene may become associated with memories of preparing dinner, supporting the recall of those memories. Instead, you could run errands in a new shopping mall. You may have difficulty recalling all the items purchased since you were rapidly switching between each new store. Prior research showed how memory performance is influenced by several different qualia of context, including perceptual attributes (Heusser et al., 2018), task set (Polyn et al., 2009b), and stimulus class (DuBrow & Davachi, 2013, 2016). Questions remain about how the qualitative features of context change influence memory structure and organization.

There are two particular features of contextual change known to influence memory but have yet to be studied in the context of free recall: rate of context changes and relative novelty of the context to which one is switching. Typically, when an item is presented during study, it is stamped into a continuously drifting context representation. The detection of a sufficiently novel representation, however, can cause a sudden shift in context (Polyn et al., 2009a). When slowly alternating between different contexts, the internal context that tags individual items is highly differentiated, which has been shown to provide structure for participants' free recall (Heusser et al., 2018; Polyn et al., 2009b). However, when rapidly switching between two repeated contexts, part of the prior context may not only linger into the new context at transitions, but also overlap, creating a "blended" contextual representation. Little is known about whether a "blended" internal context representation would be beneficial or detrimental for free recall memory.

One possibility is that recall accuracy would benefit from rapid contextual switching as items will be more easily recalled if tagged with more varied contexts, providing more contextual retrieval cues (Lohnas et al., 2011; Siegel & Kahana, 2014). However, recall could also be impaired due to interference from overlapping memories that share similar internal context representations. When memories share features, retrieving those memories may be more difficult compared to memories that do not share features due to heightened competition during retrieval (Anderson, 2003). The current set of experiments was designed to arbitrate between these two hypotheses.

The factors that contribute to a "blended" context may not solely rely on the frequency of switching, but could also be modulated by the learner's familiarity with the contexts. Accumulating evidence suggests that salient events, like encountering a novel scene (Zacks & Swallow, 2007) or oddball items (Ranganath & Rainer, 2003; Von Restoroff, 1933), can separate the overlap amongst two contexts and boost memory performance. However, increasing the amount of novelty or frequency of novel events leads to worse memory performance (Radvansky et al., 2011; Reggev et al., 2018; Shepherdson, 2021) and less access to information immediately following the shift (Dux & Marois, 2009). These findings lend us to expect that recall memory would be impaired specifically when individuals are rapidly switching to novel vs. repeated events due to less access to retrieval cues.

One mechanism by which switch rate may influence recall performance is by inducing competition during memory search between items learned with contexts that are switching vs. not switching. With a limited time to recall, the most memorable items will "win". When an item "wins" this competition, the context representation is updated and the next item recalled will likely have been encoded with a similar context (Lohnas et al., 2015; Lohnas & Kahana, 2014; Polyn et al., 2009a). A related, yet parallel question will investigate whether the presence of competition during memory search (competitive vs. pure lists) differentially influences memory performance when switching contexts at different rates.

This present study uses a context switching paradigm in which we independently manipulate switching rate and relative novelty of the contexts. We sought to characterize how these qualitatively different features of context change influence how well items are remembered and organized. We predict that memory will be differentially affected by switch rate with exposure to novel contexts, such that rapidly switching to novel contexts will be more harmful for memory compared to slower switching as participants may have less access to retrieval cues. We also predict that returning to a repeated context may independently benefit memory as a "blended" context could provide more contextual retrieval cues. We then determine the extent to which items are organized by the order in which they were encoded or the type of context with which they were originally presented.

Experiment 1

Methods

Participants

One hundred and ten participants from the University of Oregon completed this experiment online for course credit. One participant was excluded for chance-level performance on the encoding task, 19 participants were excluded for failing to provide audio usable for verbal recall, and six participants were excluded for writing down words as indicated on a post-experiment questionnaire. The final sample size for analysis was 84 participants (65 female, mean age 19.46 +/- 3.17 SD). Participants were randomly assigned to one of two contextual familiarity groups (repeated = 41; novel = 43). Sample size was determined based on standards in the literature of free recall (for example Polyn et al., 2009a) and doubled given that this study has a between-subjects manipulation. Consent was obtained in a manner approved by University of Oregon's Institutional Review Board.

Stimuli

In brief, encoding consisted of alternating presentations of word and scene stimuli. Scene stimuli consisted of 46 unique scene contexts, where half depicted an indoor scene and half depicted an outdoor scene (Chang et al., 2019). A scene context is defined as the image immediately preceding a particular study item (word). We randomized the presentation of scene contexts appearing in each condition across participants. Cue words were 240 two-syllable nouns presented in capitalized letters (e.g., "GIRAFFE"). Nouns were based on object image labels from the Bank of Standardized Stimuli (Brodeur et al., 2014). Words were randomly assigned to scenes and conditions uniquely for each participant. Stimuli were presented using Inquisit 6 [computer software]. (2020). Retrieved from https://www.millisecond.com.

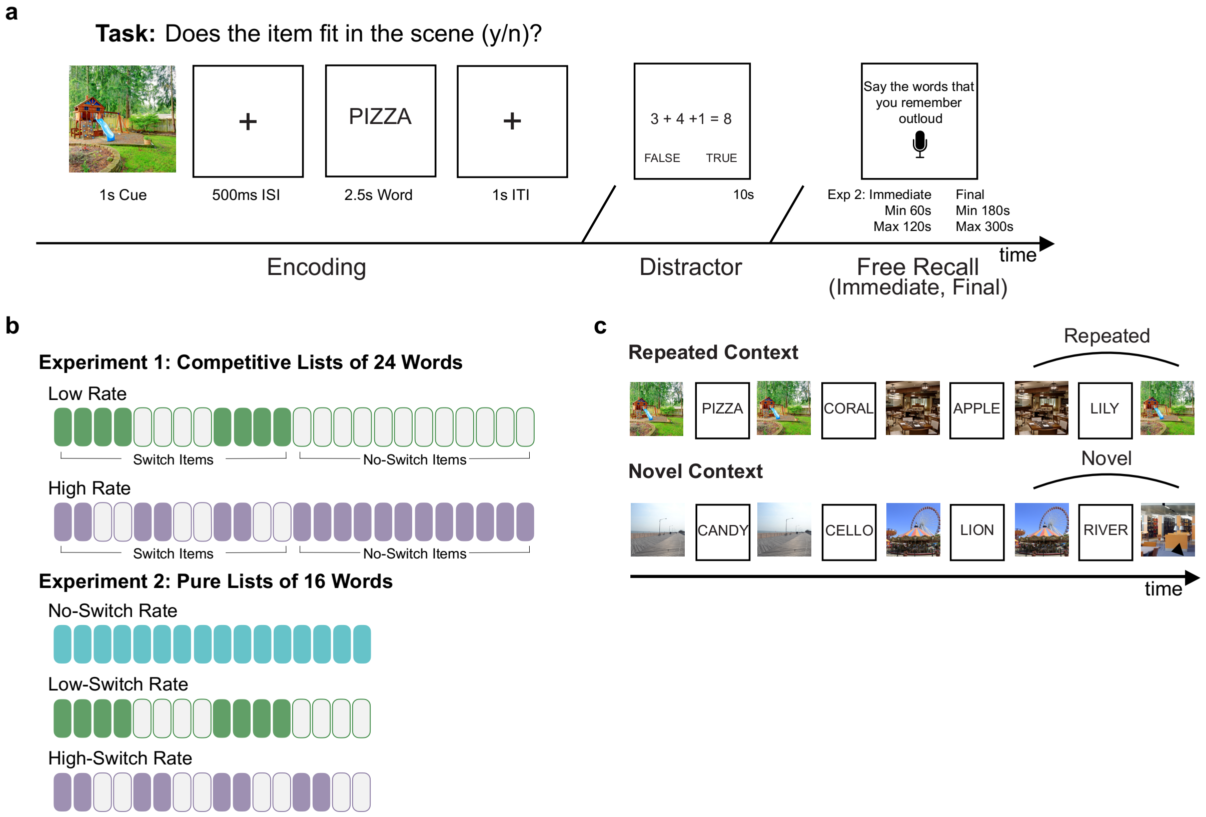

Figure 2.1. Task design for experiments 1 & 2. **a)** Procedure. Each trial began with the encoding phase, which consisted of alternating presentations of word and scene stimuli. Participants were instructed to respond as to whether the item depicted by the word would fit in the scene. After a 10s distractor task, participants verbally recalled as many items as possible from the list that they could. After all eight lists were completed, participants completed a final recall. **b)** Within Subjects Switch Rate Manipulation. In Experiment 1, participants learned lists with a high or low contextual switch rate. These were competitive lists with two switch types per list (switch vs. no-switch). In Experiment 2, participants learned pure lists at just one switch rate (no vs. low vs. high). Participants in Experiment 1 learned lists of 24 words, whereas participants in Experiment 2 learned lists of 16 words. **c)** Between Subjects Contextual Familiarity Manipulation. We manipulated the level of contextual familiarity with the scene contexts (repeated vs. novel).

Procedure

After a brief practice, the experiment consisted of eight lists, with each list consisting of three sequential phases: encoding, distractor, and recall (Figure 2.1a). On each trial, participants viewed a scene context for 1,000ms. The scene disappeared for 500ms and was then followed by a word presented in the center of the screen for 2,500ms. Alternating presentations of scene and word stimuli were chosen as it has previously been shown as an effective way to manipulate temporal context (Chan et al., 2017; Manning et al., 2016). During the word presentation, participants were instructed to respond as to whether the item depicted by the word would fit in the previous scene (yes/no). This is a subjective judgment as to whether the participant could picture a given item in the scene previously presented, which did not contain the item. The word remained on the screen for 2,500ms regardless of a button press to equate encoding time. Trials were separated by a 1,000ms intertrial interval (ITI) which consisted of a blank screen. Each list in the encoding phase included a total of 24 words.

Immediately following each encoding phase, participants completed a math distractor task to reduce rehearsal. Participants were presented with math equations in the form of A + B + C = D, where the values of A, B, and C were set to single digit integers (Howard & Kahana, 1999). Participants were instructed to indicate whether the statement was true or false with a key press. The distractor phase lasted 10s in total, but the number of equations completed was variable depending on speed of completion.

After the distraction period, participants were given up to three minutes to verbally recall as many items as possible from the list that they could, without any explicit instructions about the order of the of recall. A written cue indicated the start of the recall period, and participants' microphones were turned on for recording. Participants could move onto the next list whenever they felt that they recalled as many words as they could remember. After all eight lists were completed, participants moved onto the final recall portion of the experiment. Participants were instructed to verbally recall as many words as they could from the entire experiment for up to three minutes.

Design

The encoding task contained two main conditions of interest. For the first condition of interest, we manipulated the switch rate between scenes to generate two switch rates within subjects: low rate and high rate (Figure 2.1b). For the low rate, the scene contexts changed after every four items. The high rate was the most rapid switch rate, where the scene context switched after every two items. Each list had two different switch types within the list: switch (high or low) and no-switch (Figure 2.1b). The no-switch rate (baseline) is the slowest switch rate, where all of the items were studied with the same scene (no context switches). The rationale was to create competitive lists and to include a baseline, no-switch rate for comparison within each list. Therefore, given that a list was composed of 24 unique items, 12 are presented at the no-switch rate and 12 are presented at the switch rate (either the low-switch or high-switch rate). List order and switch type order was randomized for each participant.

The second condition of interest is the level of contextual familiarity that participants have with the scene contexts. We manipulated contextual familiarity (repeated vs. novel) as a between-subjects variable (Figure 2.1c). Within a given list in the repeated context condition, participants switched back and forth between the same two scene contexts (see Figure 2.1b for example list). In other words, when there was a change in the scene context, it would be a repeat of a scene that had already been seen in the list previously. However, in the novel context condition, each time there was a switch in scene context, participants would see a novel scene that had not been seen before in the experiment. In both groups, every list contained new scenes and included both switch and no-switch items.

Data analysis

Statistical analyses were conducted in R 3.6.3 (R Core Team (2020); https://www.R-project.org/). For the encoding task, given the subjectivity of responses, accuracy was calculated based on normative responses. We determined whether each response matched the modal response for when each word was presented with each scene. Mean responses were calculated for each level of contextual familiarity and compared using Welch's Two Sample t-tests, as there are unequal sample sizes. Effect sizes (e.g., Cohen's d) were calculated using the *lsr* package in R.

Using the *lme4* package in R, Generalized Linear Mixed-Effects Models were used to determine whether switch rate (low vs. high), switch type (no-switch vs. switch) and contextual familiarity (repeated vs. novel) predicted the percent of words that participants recalled, with subject and word identity as random effects. Specifically, we ran a model that assessed the relationship between percent of words recalled and the interaction between switch rate, switch type, and contextual familiarity. In a parallel question, we were interested in how the nature of competition between switch rates during memory search influences memory performance. Therefore, we ran an additional model that further unpacked the two-way interaction between switch rate and switch type. Given that our main predictions were about the high-switch rate, we ran a third model that specifically looked at the two-way interaction between high-switch rate and contextual familiarity (repeated vs. novel) to better interpret this interaction. These analyses were run for both immediate and final recall data (see Supplementary Figure 2.1 for final recall results).

Additionally, we ran a final model to determine whether item position in the event predicted the percent of words that participants recalled (see Supplementary Analysis 1). All models additionally controlled for list number and list half (whether the word appeared in the first 12 or last 12 items in the list) as fixed effects.

To determine the extent to which participants tend to successively recall nearby items, we calculated a temporal clustering score for each participant (Polyn et al., 2009a). For each recall transition, we determined the temporal distance (in absolute lag) between the serial position of the just-recalled word and the set of not-yet-recalled words. The temporal clustering score is calculated as the proportion of possible lags greater than the observed lag. A score of 1 indicates high temporal clustering, meaning that participants made the shortest transitions possible. A score of 0.5 indicates chance-level temporal clustering, meaning that transitions were just as likely to be to a neighboring or remote item. For this analysis, each participant received two temporal clustering scores: one for high rate lists (which includes both the switch and no-switch items) and one for low rate lists (which includes both the switch and no-switch items). Temporal clustering scores were computed using publicly available MATLAB (The MathWorks, Natick, MA) scripts from the Behavioral Toolbox (Version 1.01) from the Computational Memory Lab (http://memory.psych.upenn.edu/Behavioral_toolbox). Mean temporal clustering scores were calculated and compared across levels of contextual familiarity (repeated vs. novel) using t-tests.

Verbal recall responses were digitally recorded and annotated offline using Penn Total Recall (http://memory.psych.upenn.edu/TotalRecall). Four undergraduate research assistants, who were blind to which words were randomly assigned to which switch rate and level of contextual familiarity (repeated vs. novel), annotated the verbal responses. A recall was classified as valid if the item recalled came from the current list. Items from previous lists, words not in the wordpool, or other vocalizations (e.g, “umm”) were not included in analysis.

Results

Encoding performance

Overall accuracy was 87.71%. Accuracy and response time (RT) did not differ for repeated and novel context switches (Accuracy: repeated- $M = 87.72\%$, $SE = 0.96$, novel- $M = 87.71\%$, $SE = 0.9$, $t(81.42) = 0.01$, $p = .99$, $d = .002$; RT: $F(1, 82) = 1.42$, $p = .24$, $d = .11$).

Context switching and immediate recall performance

Participants recalled 22.37% of total words. Free recall accuracy was greater for repeated (24.45%) vs. novel (20.39%) switches, $t(81.99) = 2.18$, $p = .03$, $d = .48$, suggesting that participants’ memory was better for words from lists containing repeated scenes.

We next examined whether switch rate, switch type, and contextual familiarity influenced recall performance. There was a significant three-way interaction, highlighting that the relationship between switch rate (high vs. low) and switch type (no-switch vs. switch) differed depending on whether scenes were repeating or novel, $z = -2.48$, $p = .01$, partial $R^2 < .001$ (see Supplementary Table 2.1 for full model).

Next, we unpacked the two-way interaction between switch rate and switch type. With exposure to novel contexts, recall performance was reduced when switching contexts at a high rate, compared to not switching, $z = 3.26$, $p = .001$, partial $R^2 = .003$ (Figure 2.2a). There was no detriment to memory for low-switch, compared to no-switch, items with novel context switching, $z = .30$, $p = .76$, partial $R^2 = .001$. This resulted in a reliable high x low rate interaction, which highlights that performance is disrupted only when switching to novel contexts at a high rate, $z = 2.05$, $p = .04$, partial $R^2 < .001$. Interestingly, there was a boost in recall performance for high-switch, over no-switch, items when switching back to repeated contexts, $z = 2.83$, $p = .005$, partial $R^2 = .001$ (Figure 2.2a).

Given that performance differences were specific to rapid switching, a final analysis was conducted to directly test the interaction between high-switch rate and contextual familiarity. This resulted in a reliable high rate x context familiarity interaction, $z = 4.21$, $p < .001$, partial $R^2 = .002$ (Figure 2.2a). This means that switching back to repeated contexts at a rapid rate may rescue the cost associated with rapidly switching to novel contexts.

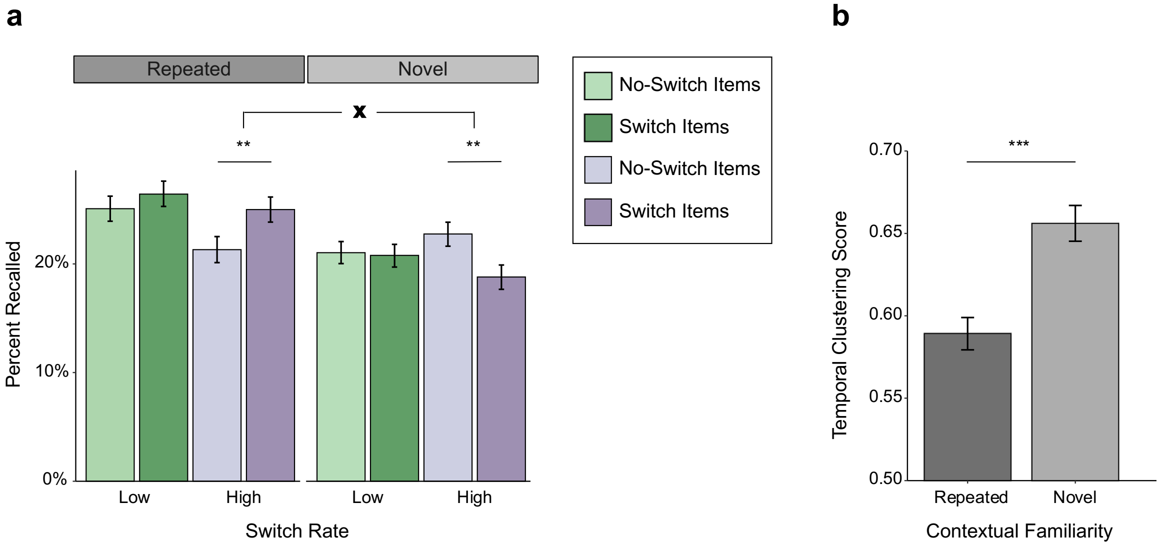

Figure 2.2. Experiment 1 results. a) Immediate Recall Performance. **b)** Temporal Clustering. Error bars reflect within subject standard error. ** $p < .01$, *** $p <.001$.

Context switching and recall organization

We next investigated how switch rate and contextual familiarity influenced temporal organization. Results showed that both switch rates across both levels of familiarity showed significant binding of items to their temporal context, as measured by greater than chance-level temporal clustering (*ps* < .001). However, when individuals were switching to novel vs. repeated contexts, there was a greater reliance on temporal information (i.e., higher temporal clustering), $t(157.6) = 4.99$, $p < .001$, $d = .77$ (Figure 2.2b).

Experiment 1: Discussion

The results suggest that costs to memory only occur when individuals are rapidly switching to novel contexts. In fact, participants' memory performance was improved when rapidly switching to repeated contexts over not switching. This suggests not only a benefit for switching to repeated contexts, but that impairments of switching to novel environments only emerged in the context of rapid versus slower switches.

Experiment 1 used competitive lists (containing both switch and no-switch items) to test how competition between switch and no-switch items during memory search influenced memory performance. Results demonstrated that this competition shaped memory performance. First, performance for no-switch items differed depending on switch rate (high vs. low), given that no-switch items were competing with different switching rates in memory. Additionally, memory differences between switch and no-switch items were only observed in high-switch rate lists. For Experiment 2, we will investigate whether competition between switch rates was necessary to observe memory differences.

We additionally found that switching to novel contexts was more likely to increase reliance on temporal information. This may seem counterintuitive as recall performance is disrupted at a high switch rate to novel contexts, supporting the idea that participants may be making more remote transitions when switching to repeated contexts. These findings support the framework that when scenes are repeatedly encountered, a “blended” context representation is created that spans the entire list, supporting long-distance transitions. We quantitatively test this in Experiment 2 by further investigating the types of recall transitions made by participants.

Experiment 2

Experiment 2 aimed to replicate the above findings with increased sample size and recall performance. The goals for Experiment 2 were: 1) replicate the recall performance findings that the negative effect of switching on memory recall was rescued (at least as good as not switching) when switching to a repeated context and 2) replicate and expand on the recall organization results to further investigate how participants structure their memory. To expand, we investigated the types of recall transitions participants made.

Methods

Participants

One hundred ninety-two native English speakers were recruited from Prolific. In order to increase power for Experiment 2, we doubled the sample size from Experiment 1. Participants were compensated an initial \$6.50 and could receive an additional bonus payment of up to \$6.00 for good performance on the encoding and recall portions of the experiment. Nine participants were excluded for chance-level performance on the encoding task, six participants were excluded for failing to provide audio usable for verbal recall, and ten participants were excluded for writing down words as indicated on a post-experiment questionnaire. The final sample size for analysis was 167 participants (90 female, mean age 35.74 +/- 12.98 SD). Participants were randomly assigned to one of two context switching groups (repeated = 83; novel = 84). Consent was obtained in a manner approved by University of Oregon's Institutional Review Board.

Stimuli

The stimuli used for Experiment 2 were the same as those used in Experiment 1. However, in Experiment 2, we only used 30 of the scene contexts as the list length was shortened (see below).

Design & procedure

The procedure for Experiment 2 was identical to that of Experiment 1, except for the following changes aimed at improving participants' verbal recall performance. The first set of changes were made to the encoding portion of the experiment. First, the list length was shortened to only contain 16 items per list. The rationale for this change was to help improve recall performance. Second, given that the lists were shorter, the switch rate variable changed such that there are now three distinct switch rates (no-switch, low-switch, and high-switch) presented in their own list to optimize the number of switch items per condition. Thus, participants learned pure lists where there was no competition between switch rates during memory search as each rate was learned and tested separately. This allowed for investigating whether competition is necessary for observing differences in recall performance between switch rates as no competition is present in Experiment 2. Additionally, this eliminated the switch type variable. Participants saw two lists of each switch rate for a total of six lists. One additional change was made in the instructions to improve the clarity of the encoding task and create a more even distribution of yes/no responses. Participants were completing the same encoding task as Experiment 1, but were now instructed to make a yes/no judgment as to whether they could find the item in the scene.

We also changed the recall portion of the experiment. In Experiment 1, participants could move onto the next list whenever they felt that they recalled as many words as they could remember. However, in Experiment 2, a minimum time was added to the immediate and final recall. The instructions were changed to encourage participants to continue to search their memory until at least the minimum time was up. After the minimum time was up, participants could move onto the next list, or continue to search their memory until the maximum time has passed. For immediate recall, participants had up to two minutes to recall, but would not be allowed to continue until after one minute. For final recall, participants had up to five minutes to recall, but would not be allowed to continue until after three minutes. This change was aimed at increasing recall performance by preventing participants from recalling just a few words and moving on and rather encouraging them to really search their memory.

Data analysis

Data analysis was identical to Experiment 1 with the following changes and additions. First, given that Experiment 2 used pure lists, the switch type variable is eliminated from analyses. Therefore, Generalized Linear Mixed-Effects Models were used to determine whether switch rate (no-switch vs. low-switch vs. high-switch) and contextual familiarity (repeated vs. novel) predicted the percent of words that participants recalled, with subject and word identity as random effects. Specifically, we ran a model that assessed the relationship between percent of words recalled and the interaction between switch rate and context familiarity. As in Experiment 1, these analyses were run for both immediate and final recall data (see Supplementary Figure 2.1 for final recall results), and all models additionally controlled for list number and list half as fixed effects.

Additionally, we sought to determine the extent to which participants successively recalled items shown with the same scene, or source context. During the encoding task, items (represented by words) were paired with the scene context immediately preceding. We were interested in the question: When a participant makes a local transition during recall, how often is it to the same or a neighboring context? There are three types of local transitions. Same context transitions were when participants made their next recall to an item paired with the same context as the context of the just-recalled item. Backward context transitions were when participants made their next recall to an item paired with the context immediately preceding (backwards) the context of the just-recalled item. Lastly, forward context transitions were when participants made their next recall to the item paired with context immediately following (forwards) the context of the just-recalled item. Only local transitions were analyzed as this is a fair comparison between switching to repeated vs. novel contexts (see Supplementary Analysis 2 for further investigation into local and remote transitions). Inclusion of remote transitions would allow participants switching to repeated contexts to transition between items paired with the same scene throughout in the list, which was not possible when switching to novel contexts. Therefore, inclusion of only local transitions allowed for an analysis of the same types of transitions for lists with repeated and novel contexts.

For this analysis, we calculated the conditional response probabilities by local context type, similar to (Polyn et al., 2009a). For each participant, we tallied the number of recall transitions that were between items studied with the same image, the previous image (backwards transition), and the following image (forwards transition). We then conducted two different analyses: 1) To account for differences in the number of transitions each participant made, we divided each context type by each participant's total number of recall transitions. This gave the proportion of local transitions for each participant that was then averaged across all participants in each group (see

Supplementary Figure 2.2). 2) Separately, to account for the fact that there were a different number of opportunities to transition to each context type (same, forward, or backward), the number of recalls from each type was divided by the total number of recall transitions possible for that type. This gave the probability of local transitions for each participant that was then averaged across all participants per type.

Here, we were interested in how organization by source context differed between repeated and novel context switches, within each switch rate. Therefore, we used the *lme4* package in R to run Linear Mixed-Effects Models to make such comparisons. The high-switch and low-switch rates had a different number of items between each transition (2 vs. 4 items), so therefore it would not make sense to compare these two rates, as the number of potential switch transitions differs across rates. Thus, we ran two separate models, one for the low-switch rate comparing repeated vs. novel context switches and one for the high-switch rate again comparing repeated vs. novel context switches. Additionally, this analysis was unable to be run in Experiment 1 because within a given list, recalls included items from both a no-switch and a switching (low-switch or high-switch) rate. Therefore, transitions between items are not matched.

Results

Encoding performance

Overall accuracy was 85.3%. Accuracy and RT did not differ between repeated and novel switches (Accuracy: repeated- *M* = 84.61%, *SE* = 0.94, novel- *M* = 85.99%, *SE* = 0.64, *t*(158.27) = 1.13, *p* = .26, *d* = .17; RT: *F*(1, 165) = 1.47, *p* = .23, *d* = .09).

Context switching and immediate recall performance

Participants recalled 50.47% of total words. There were no differences in the percent of words recalled between repeated (51.15%) and novel (49.79%) switches, $t(164.97) = .51$, $p = .61$, $d = .08$. This demonstrates that design changes made in Experiment 2 were successful in raising recall performance and equating overall accuracy across levels of contextual familiarity.

We next tested for interactive effects of switch rate (no-switch vs. low-switch vs. high-switch) and contextual familiarity (repeated vs. novel). Replicating Experiment 1, rapidly switching to novel, $z = -2.64$, $p = .008$, partial $R^2 = .001$, but not repeated, contexts reduced memory performance and resulted in a reliable interaction, $z = 2.19$, $p = .03$, partial $R^2 = .001$ (Figure 2.3). There were no performance differences for low-switch between repeated and novel contexts, $z = .07$, $p = .94$, partial $R^2 < .001$. As expected, recall performance when not switching was similar between novel and repeated contexts, $z = -.003$, $p = .99$, partial $R^2 = .001$, since there was no competition between rates in memory search. Thus, we directly replicated that memory recall is hindered *only* when switching to novel contexts at a high rate.

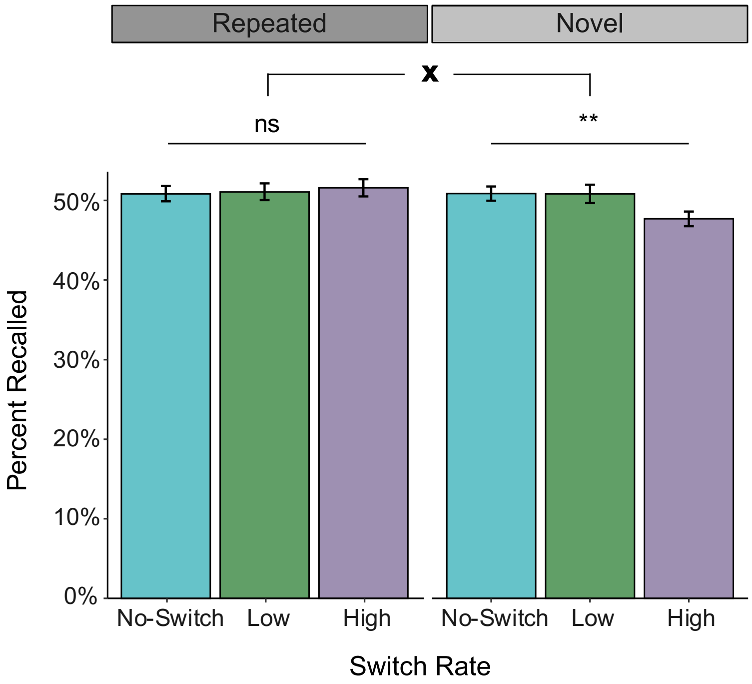

Figure 2.3. Experiment 2 immediate recall performance. Error bars reflect across subject standard error. ns $p > .05$, ** $p < .01$.

Context switching and recall organization

Temporal clustering. Results showed that all switch rates across both levels of contextual familiarity exhibited greater than chance-level temporal clustering (*ps* < .001). Replicating results from Experiment 1, there was greater reliance on temporal information (i.e., higher temporal clustering) when switching to novel, compared to repeated, contexts, $t(330.14) = 3.07$, $p = .002$, $d = .34$ (Figure 2.4a).

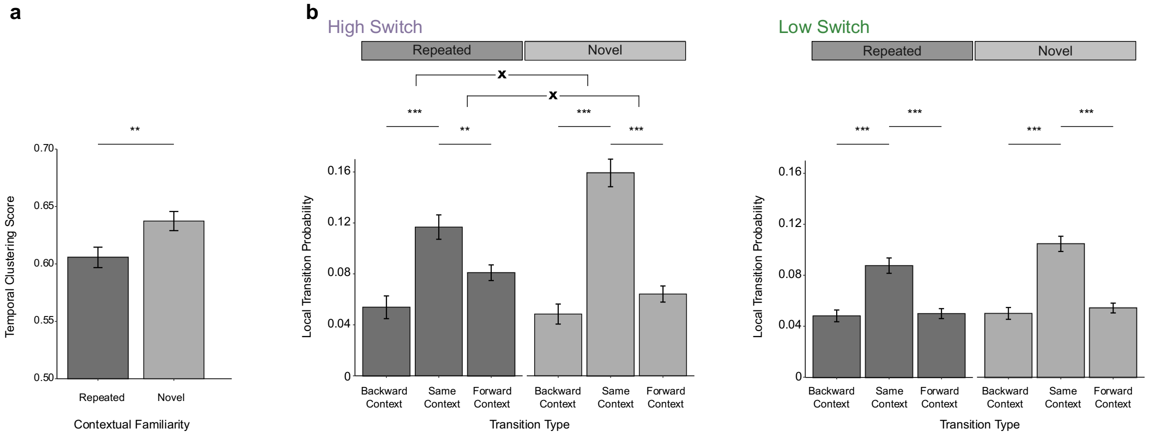

Figure 2.4. Context switching and recall organization. a) Temporal Clustering. **b)** Probability of Local Recall Transitions by Context for High-Switch (left) and Low-Switch (right) Rates. Here we calculated the probability of making a local transition compared to the number of possible transitions per type. The low-switch and high-switch results are unable to be directly compared due to differences in the number of items between each transition (2 vs. 4 items). The main comparison of interest is between repeated and novel context switches within switch rates. Error bars reflect across subject standard error. ** *p* < .01, *** *p* <.001.

Recall transitions by context. One reason that performance differences were specific to switching at a high rate may be differences in how participants organized their memory. Therefore, this next analysis examined the proportion of recall transitions made to the same or neighboring contexts (forwards or backwards). At the high-switch rate, participants transitioned significantly more to items in the same context compared to neighboring contexts when switching to repeated, (Forwards: t(164.0) = 3.03, p = .002, partial R^2 = .029, Backwards: t(164.00) = 5.33, p < .001, partial R^2 = .085) and novel (Forwards: t(166.0) = 7.87, p < .001, partial R^2 = .177, Backwards: t(166.0) = 9.17, p < .001, partial R^2 = .226) contexts. Although all participants made most of their recall transitions to the same context, there was a significant interaction such that there was less of a difference in the probability of making same vs. forward, t(330.0) = 3.503, p <.001, partial R^2 = .020, or same vs. backward, t(330.0) = 2.83, p = .004, partial R^2 = .013, context transitions when participants were switching to repeated, compared to novel, contexts (Figure 2.4b). This demonstrates a notable difference in how participants switching between repeated vs. novel contexts organize their recalls when switching at a high rate.

For the low-switch rate, participants transitioned significantly more to items in the same context compared to neighboring contexts in repeated, (Forwards: $t(246) = 6.85$, $p < .001$, partial $R^2 = .163$, Backwards: $t(246) = 7.13$, $p < .001$, partial $R^2 = .174$), and novel contexts, (Forwards: $t(249) = 9.68$, $p < .001$ partial $R^2 = .277$, Backwards: $t(249) = 9.90$, $p < .001$, partial $R^2 = .287$; Figure 2.4b). There were no significant differences between repeated and novel switches.

Experiment 2: Discussion

Replicating Experiment 1, results demonstrated that memory was hindered only when switching to novel contexts at a high rate, highlighting a unique function of rapid switching on memory performance. Additionally, although there was no direct memory benefit, memory for items during repeated context switches was just as good as memory with no context switches, reducing the costs associating with rapidly switching to novel contexts.

Experiment 2 used pure lists (no competition between switch and no-switch items) to test whether competition was necessary to see differences in memory performance between switch rates, as in Experiment 1. First, as there was no boost in memory performance for either the high-switch or the low-switch rates above the no-switch rate for repeated context switches, this suggests that competition between switch and no-switch items during memory search is an important component for boosting switch items in memory. However, replicating Experiment 1, rapidly switching to novel contexts hindered memory performance, compared to not switching, suggesting that regardless of list composition, rapidly switching to novel contexts is harmful for memory recall performance.

General Discussion

Across two experiments, we investigated free recall performance and organization after manipulating the rate and familiarity of context switches. Consistent with our hypothesis, we found and replicated that memory was differentially affected by switch rate with exposure to novel contexts, where there was a recall detriment only when switching at a rapid rate. However, this detriment was not observed when participants switched rapidly between repeated contexts, suggesting that rapidly switching between repeated contexts may rescue the cost associated with rapidly switching to novel contexts. We also found that relative novelty of the contexts shaped recall organization. Participants who switched to novel contexts relied more heavily on temporal information. On the other hand, when participants rapidly switched to repeated contexts, they were less likely to only cluster their responses by the same context.

The results of both experiments add to a growing body of literature characterizing the effects of switching contexts on free recall performance and organization. Previous studies found that a single change in task set (Polyn et al., 2009b) or slowly changing perceptual features (Heusser et al., 2018) during learning are sufficient to impose structure on free recall, where more transitions were made between items studied using the same task compared to different tasks. Our findings from the low-switch rate are consistent with this result. We extend to suggest that clustering by scene context may be switch rate dependent. Specifically, participants are less likely to only cluster their responses by context during rapid switching to repeated, compared to novel, contexts. Our results also replicate previous findings that participants tend to recall information in a similar temporal order in which it was learned. We extend these findings by showing that temporal clustering is heightened during novel context switching. In certain situations, clustering items by their temporal context may not be as adaptive, where participants may have more success grouping items by contextual, semantic, or motivational relationships between items (Horwath et al., 2023; Howard & Kahana, 2002; Polyn et al., 2009a). However, in situations when such relational information may be unavailable or changing too quickly, participants may rely more on remembering the items in their studied order.

Importantly, and adding to prior work on novelty and memory, we demonstrate that the cost of switching to novel events is specific to switching at a high rate. This is consistent with previous work where increasing the amount of novelty leads to worse memory performance (Radvansky et al., 2011; Reggev et al., 2018; Shepherdson, 2021). Here, participants may become overloaded with new, quickly changing information which influences their ability to remember specific items. For instance, research suggests that novelty-related context disruption may reduce accessibility for items studied prior to the novel events (Polyn et al., 2009a). However, the detriment was eliminated when participants slowly changed to new information. An open question for future work is to understand why slowly switching to novel contexts does not hinder free recall. The findings from the present experiments highlight the importance of the rate at which individuals switch to novel environments. Moreover, the number of switches per list may also be relevant for disrupting memory. Future research should further disentangle how the number vs. rate of context switches influences memory.

Our findings also support a clear memory distinction between switching to repeated vs. novel contexts. Across both experiments, we found a cost for switching to novel contexts at a high frequency that was not present when switching to repeated contexts. In fact, memory performance after rapidly switching between repeated contexts was just as good as not switching. This suggests that rapidly switching to repeated contexts may rescue the costs of rapidly switching to novel contexts. A similar result was found in previous work, where participants demonstrated worse memory for an item they were carrying if they walked through multiple novel rooms compared to returning back to the same room (Radvansky et al., 2011). Here, we provide novel evidence for this memory effect after multiple switches using a free recall paradigm.

One explanation for these differences in recall performance may be due to effects of context change. Context plays an important role in guiding free recall, where the success of memory search is a function of the overlap between contextual representations at test and contextual features during encoding (Godden & Baddeley, 1975; Howard & Kahana, 2002; Smith et al., 1978; Smith & Vela, 2001). Therefore, one possibility is that novel context switches create a larger mismatch in contextual representations between encoding and test, given the greater number of scene changes. This is supported by evidence suggesting that a change in mental context impairs recall of the list prior to the context change, given that the prior list no longer matches the test context, but benefits memory for the following list which better matches the test context (Delaney et al., 2010; Mulji & Bodner, 2010; Sahakyan et al., 2013; Sahakyan & Kelley, 2002). The current findings and interpretations shed additional light for why some context change manipulations impair vs. improve recall performance.

Lastly, results demonstrated that when participants were rapidly switching to repeated contexts, the likelihood of recalling the next item from the same context relative to the likelihood of recalling an item from a neighboring context is more similar than when participants were switching to novel contexts. Thus, when participants switch to repeated, compared to novel, contexts, they were less likely to recall their next item from the same context. Therefore, the next item a participant recalls is more likely to come from neighboring contexts when switching to repeated, compared to novel, contexts. Despite these items being paired with two different external contexts, this would suggest that they are encoded with a similar, “blended” internal context representation, given that individuals are more likely to successively recall items encoded with a similar context representation (Polyn et al., 2009a). As expected, a “blended” representation is specific to repeated contexts, as there is less of a cost for thinking about the first context into the second context. During continuous switching, the first and second contexts are both active and can be used to access memories for unique items. Alternatively, having many contexts continuously active could lead to interference during novel context switches. Moreover, previous research using a similar analysis to the present study found that in lists with a single task switch, participants were more likely to recall their next item from the same task (Polyn et al., 2009a), suggesting that this framework is specific for context switching at a higher frequency. The present results begin to suggest that creating a “blended” context representation may serve as a better retrieval cue with repeated contexts compared to contexts with high amounts of novelty. Future working using neuroimaging techniques can better understand internal context representations during rapid context switching and how that influences memory structure and performance.

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CHAPTER III

HIPPOCAMPAL DRIFT RATE REFLECTS THE TEMPORAL ORGANIZATION OF MEMORIES

This chapter is submitted for publication by Lindsay I. Rait, Wanjia Guo, Zhifang Ye, Sarah DuBrow, and Brice A. Kuhl

Introduction

When freely recalling events from the past, humans tend to cluster these events based on the temporal proximity with which they were experienced. In other words, events that are experienced nearby in time tend to be recalled together (Kahana, 1996; Polyn et al., 2009; Sederberg et al., 2010). This phenomenon—temporal clustering—has been a primary inspiration for an influential class of computation models (*temporal context models*) which argue that events are encoded in relation to a slowly drifting internal context representation (Howard & Kahana, 2002; Polyn et al., 2009; Sederberg et al., 2008). The idea behind these models is that if context representations drift slowly, then successive events will be associated with a relatively shared (or stable) context. Later, when one event is recalled from memory, this activates the shared context, thereby cueing recall of other events linked to this context (i.e., temporal clustering). While temporal context models have had an enormous influence on the field of episodic memory, there remains surprisingly limited evidence directly linking temporal clustering in recall to putative neural measures of drifting context representations.

Several lines of evidence support the idea that neural activity patterns drift slowly and, critically, that this drift is relevant to episodic memory (DuBrow et al., 2017). For example, when freely recalling a stimulus from memory, electrophysiological measures of neural activity resemble not only the activity pattern that was evoked when that stimulus was originally encoded, but also the activity patterns of stimuli that were encoded nearby in time (Manning et al., 2011). Similarly, successful recognition of a previously-encountered stimulus triggers a ‘jump back’ to electrophysiological activity patterns that were *temporally adjacent* to the original encoding of that stimulus (Howard et al., 2012). This gradually drifting activity has been specifically observed within the hippocampus in studies using single-unit recording in both rats (MacDonald et al., 2011; Manns et al., 2007) and humans (Folkerts et al., 2018). Evidence from fMRI studies has built on these observations by relating hippocampal drift to episodic memory. For example, the degree of drift in the hippocampus during the encoding of a sequence of stimuli is predictive of subsequent temporal memory judgments for those stimuli (DuBrow & Davachi, 2014; Ezzyat & Davachi, 2014; Jenkins & Ranganath, 2016). While these findings link hippocampal drift to memory for temporal context, they do not directly demonstrate a connection to the temporal organization of recall. However, they motivate the idea that the rate of hippocampal drift may also contribute to the amount of temporal clustering.

Here, we sought to directly link behavioral expressions of temporal clustering during recall to hippocampal drift rate. We addressed this in two ways: (1) we actively manipulated the rate of external context change and tested whether this induced parallel effects on temporal clustering and hippocampal drift, and (2) we correlated the degree of hippocampal drift rate with the strength of temporal clustering during recall. Motivated by recent fMRI studies which have used autocorrelation to measure the stability of hippocampal activity patterns over time (Bouffard et al., 2023; Brunec et al., 2018), we defined drift rate as the degree of autocorrelation in an fMRI time series, computed at the level of individual voxels. We predicted that a relatively higher rate of external context change would lead to both less temporal clustering in recall and less hippocampal autocorrelation. Additionally, we predicted that temporal clustering would be positively correlated with hippocampal autocorrelation (i.e., less hippocampal drift = greater temporal clustering in recall).

Methods

Participants

Thirty-nine participants from the University of Oregon and broader community were enrolled in this experiment. One participant was excluded due to technical issues during scanning that prevented completion of the experiment. The final sample size included in analyses was 38 participants (20 female, mean age 21.18 +/- 3.85 SD). The sample size was comparable to similar fMRI studies in the field. All participants received monetary compensation for their participation ($25/hr). Participants were right-handed, native-English speakers, with normal or corrected-to-normal vision, and with no self-reported psychiatric or neurological disorders. Consent was obtained in a manner approved by University of Oregon’s Institutional Review Board.

Stimuli

Stimuli consisted of 14 scene images and 192 cue words. Seven scene images depicted an indoor scene and seven depicted an outdoor scene. Scenes were color images taken from the Scene UNderstanding (SUN) database (Xiao et al., 2010). Cue words were two-syllable nouns presented in capitalized letters (e.g., “DAISY”) that were based on object image labels from the Bank of Standardized Stimuli (Brodeur et al., 2014). Scene images and cue words were randomly assigned to switch rate conditions uniquely for each participant. All stimuli were presented to participants using PsychoPy (Peirce et al., 2019).

Experimental procedure

The experimental paradigm was modeled after a recent behavioral study (Rait et al., 2024). After providing consent and reviewing the instructions, participants entered the MRI scanner. Participants first completed a brief practice task in the scanner. Then, participants completed the main experimental task, which consisted of eight rounds (each round = 1 scan run). Each round included three sequential phases: encoding, distractor, and immediate recall. Participants then completed a final recall task and two rounds of a visual category localizer task before exiting the scanner. Note: data from the final recall task and the visual category localizer are not described in the current manuscript.

During the encoding phase, scene images ('contexts') and words were alternately presented (Figure 3.1a). Specifically, each trial began with the presentation of a scene image (800 pixels by 800 pixels) in the center of the screen (1000ms), followed by a fixation cross (500ms), and then the presentation of a word in the center of the screen (2500ms). On each trial, participants were instructed indicate, using a button box in their right hand, whether or not they would be likely to find the referent of the word within the immediately-preceding scene (yes/no). Participants pressed with their index finger to make a 'yes' response and with their middle finger to make a 'no' response. Participants were instructed to make their response before the word disappeared from the screen. Responses were considered missing if late. After the word, there was a 2500ms intertrial interval (ITI) during which a fixation cross was presented. Each encoding phase included a total of 24 trials. These 24 trials always included 24 unique words and either included one or two different scene images (contexts), depending on the experimental condition (see Design). For each word, the immediately-preceding scene image was defined as the scene context.

Following each encoding phase, participants completed a math distractor task consisting of five equations for 15s in order to reduce rehearsal (Howard & Kahana, 1999). Participants were presented with math equations in the form of A + B + C = D, where the values of A, B, and C were set to single digit integers. Participants indicated whether the equation was true or false using a key press (index finger for true, middle finger for false). For false equations, the result (D) differed from the correct sum by either plus or minus one.

After the distractor task, participants saw the word "RECALL" appear on the screen, which indicated the start of the immediate recall phase. During this phase, participants were given one minute to verbally recall as many words as possible from the encoding phase of the current round. Participants were not given any explicit instructions about the order in which words should be recalled (i.e., it was a free recall task). Responses were recorded via a Persaio microphone in the scanner that was only turned on for recording during the free recall portion of the scan.

After the eight rounds of the main experimental task, participants completed a final recall task during a separate scan run. Participants were given two minutes to verbally recall as many words as they could from the entire experiment, without any explicit instruction about the order in which to recall the words. As in the immediate recall phases, responses were recorded by microphone.

Finally, participants completed a visual category localizer task (two rounds). During this task, all 14 scene images were presented ten times each (five times per round), in a randomized order. A black fixation cross was presented in the middle of the scene was red and participants were instructed to press a button whenever it turned red. Additional details of this task are not included because data from this task are not described in the current manuscript.

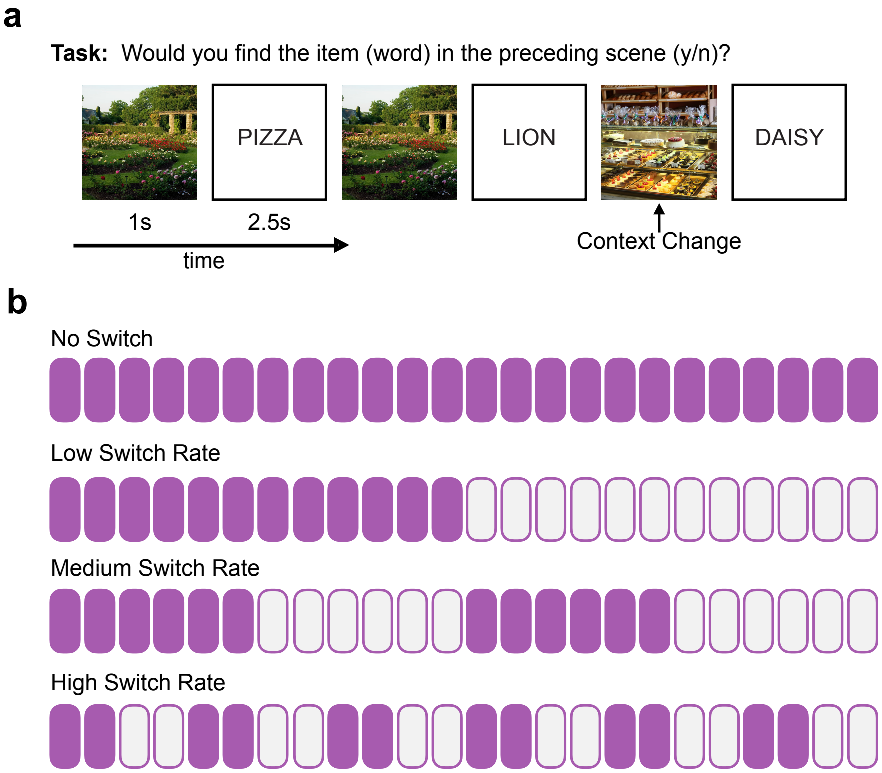

Figure 3.1. **Encoding procedure and design. a)** Overview of the encoding task. The encoding phase consisted of alternating presentations of word and scene stimuli. Participants were instructed to respond (yes/no) as to whether they would find the item (word) in the preceding scene. A context change occurs when there is a change in the scene image. **b)** Structure of encoding lists. Participants learned eight lists of 24 words each. We manipulated the rate of context change between scenes to generate four switch rate conditions within subjects. Context changes are represented by a change in fill color. The No Switch Rate acted as a baseline for comparison, where there were no context changes. The Low Switch rate had just a single context switch halfway through the list (after 12 items). For the Medium Switch rate, the scene context switched every six items, so there were three context switches. Lastly, the High Switch rate was the most rapid switch rate, where the scene context switched after every two items.

Design

For each participant, the eight rounds of the main experimental task included four different 'switch rate' conditions (2 rounds each): No Switch, Low, Medium, and High (Figure 3.1b). These conditions refer to whether the scene context changed within a given encoding phase and, if so, at what rate. For the No Switch condition, the scene context did not change within a given encoding phase (i.e., all 24 words had the same scene context). The No Switch condition was used as a baseline against which the other conditions were compared. For the Low, Medium, and High Switch conditions, each encoding phase included two scene contexts, but the rate of switching between these scene contexts varied. For the Low Switch condition, only a single context switch occurred, halfway through the encoding phase (i.e., after 12 items). For the Medium Switch condition, the scene context switched after every six words; thus, there were three context switches within each Medium Switch encoding phase. For the High Switch condition, the scene context switched after every two words; thus, there were eleven context switches in each High Switch encoding phase. The order of the four switch rate conditions was randomized for each participant with the constraint that each participant had to complete one round of each switch rate condition before a switch rate condition could be repeated. Additionally, each round contained a novel scene (No Switch condition) or pair of scenes (Low, Medium, High Switch conditions) to avoid interference across rounds.

Analysis of behavioral data

For the encoding phases, we calculated the percentage of trials for which participants responded 'yes' vs. 'no', after removing trials without a response. Mean ‘yes’ vs. ‘no’ responses were separately calculated for each switch rate condition

For the Immediate Recall phases, participants’ verbal recall responses were digitally recorded and annotated offline using Penn Total Recall (http://memory.psych.upenn.edu/TotalRecall). Four undergraduate research assistants, who were blind to which words were randomly assigned to which switch rate condition, transcribed the verbal responses. A recalled word was classified as ‘valid’ if the word was presented during the corresponding encoding phase. Intrusions (i.e., words from previous lists or not in the wordpool) or other vocalizations (e.g, “umm”) were excluded from analyses. Additionally, if participants recalled the same word more than once during an immediate recall phase, only the first recall of that word is considered a ‘valid’ recall. We considered three separate measures of memory performance from the immediate recall phases: (1) the total percentage of words recalled, (2) the percentage of boundary and pre-boundary words recalled and (3) temporal clustering.

The *total percentage of words recalled* during each round was defined as the number of ‘valid’ recall words divided by 24 (the total number of words that were encoded).

Recall for boundary and pre-boundary items was defined as recall for words that immediately followed and immediately preceded a context switch, respectively. The number of boundary/ pre-boundary items differed across the switch rate conditions. In the No Switch condition, because the scene context never switched, there were no boundary or pre-boundary items. In the Low Switch condition, there was only one boundary item and one pre-boundary items.

For the Medium Switch condition, there were three boundary and three pre-boundary items. For the High Switch condition, there were 11 boundary and 11 pre-boundary items. Recall for boundary and pre-boundary items was therefore expressed as the percentage of these items that were recalled, separately for each of the three conditions in which context switches actually occurred. Note: here we do not consider the first item in a list to be a boundary item.

For each participant, a *temporal clustering* score was computed separately for each of the 8 immediate recall phases, with scores then averaged by switch rate condition (Polyn et al., 2009a). To compute a temporal clustering score for a given study list, we first removed all 'invalid' recalls (e.g., intrusions from a prior list) so that only valid recalls remained. For each of these valid recalls (excluding the *last* recalled word), we then determined the temporal distance during the encoding phase (in absolute positional lag) between that word and the next recalled word (the 'actual lag'; see Figure 3.3a), as well as the temporal distances between that word and all other words from the encoding phase that were not yet recalled ('possible lags'). The temporal clustering score was defined as the proportion of possible lags greater than the actual lag. The highest possible temporal clustering score, therefore, would be 1. This would indicate that a participant made the shortest *possible* recall transitions. A score of 0.5 indicates chance-level temporal clustering, meaning that recall transitions were equally likely to be to a nearby vs. remote item. Temporal clustering scores were computed using publicly available MATLAB (The MathWorks, Natick, MA) scripts from the Behavioral Toolbox (Version 1.01) from the Computational Memory Lab (http://memory.psych.upenn.edu/Behavioral_toolbox). Temporal clustering scores are initially reported separately for each of the four switch rate conditions. In subsequent analyses, temporal clustering scores are expressed relative to the No Switch condition (i.e., the No Switch condition served as a baseline). Additionally, temporal clustering scores are averaged across the Low and

Medium Switch conditions and directly compared to the High Switch condition. The rationale for combining the Low and Medium Switch conditions is that these conditions were relatively similar in terms of total number of context switches per encoding phase (one vs. three switches, respectively) and each had many fewer switches than the High Switch condition (11 switches).

fMRI data acquisition

All scanning was performed on a Siemens 3T Prisma MRI system in the Lewis Center for Neuroimaging at the University of Oregon. Functional images were collected with a T2*-weighted multiband accelerated echo-planar imaging pulse sequence with partial-brain coverage (repetition time = 1500ms, echo time = 26ms, flip angle = 71°, 69 slices, 2 × 2 × 2 mm voxels) and a 64-channel head coil. Note: the total trial length during the encoding phase (6500ms) was not a multiple of the repetition time (TR). The use of an 'off-TR' design with a relatively short TR was motivated by our focus on autocorrelation in the *un-modeled* fMRI timeseries. Additionally, to maximize spatial resolution within the hippocampus and visual cortical regions, we used a high-resolution, partial field-of-view protocol. Slices were oriented parallel to the long-axis of the hippocampus, fully covering the medial temporal lobes and visual cortex, but only partially covering frontal cortex. Each scan for the main experimental task (8 total) consisted of 162 total volumes. The final recall scan (1 total) consisted of 88 total volumes. The visual category localizer scans (2 total) consisted of 170 total volumes each. All scans included 10s of lead-in time. Anatomical scans included high-resolution structural T1-weighted whole brain images (3D MPRAGE scan, 1 × 1 × 1 mm voxels) and high-resolution structural T2-weighted coronal images

(0.4 × 0.4 × 1.8 mm voxels, perpendicular to the main hippocampus axis) to facilitate segmentation of hippocampal subfields.

Anatomical data preprocessing

fMRI data preprocessing was performed using *fMRIPrep* version 21.0.1 (Esteban et al., 2019; RRID:SCR_016216), which is based on *Nipype* 1.6.1 (Gorgolewski et al., 2011; RRID:SCR_002502). The T1-weighted (T1w) image was corrected for intensity nonuniformity (INU) with N4BiasFieldCorrection54 (Tustison et al., 2010; ANTs 2.3.3, RRID: SCR_004757), and used as the T1w reference throughout the workflow. The T1w reference was skull-stripped with the antsBrainExtraction.sh workflow (ANTs) in Nipype, using OASIS30ANTs as the target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM), and gray-matter (GM) was performed on the brain-extracted T1w using fast (FSL 6.0.5.1:57b01774, RRID:SCR_002823). Brain surfaces were reconstructed using recon-all from FreeSurfer 6.0.1 (Dale et al., 1999; RRID:SCR_001847). Volume-based spatial normalization to one standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with antsRegistration (Avants et al., 2008; ANTs 2.3.3), using brain-extracted versions of both T1w reference and the T1w template. *ICBM 152 Nonlinear Asymmetrical template version 2009c* was selected for spatial normalization (Fonov et al., 2009; RRID:SCR_008796; TemplateFlow ID: MNI152NLin2009cAsym).

Functional data preprocessing

The following preprocessing steps were performed for each of the functional scans for the main experimental rounds (8 total) for each participant using *fMRIPrep*. First, a reference volume and its skull stripped version were generated by aligning and averaging one single-band reference image (SBRefs). To correct for susceptibility distortions, a field map was estimated based on two (or more) echo-planar imaging (EPI) references. The corresponding phase-maps were phase-unwrapped with topup (FSL 6.0.5.1:57b01774). The estimated field maps were then aligned with rigid-registration to the target EPI reference run. The field coefficients were mapped onto the reference EPI using the corresponding transform. Functional runs were slice-time corrected to half of slice acquisition range using 3dTshift from AFNI (Cox & Hyde, 1997; RRID:SCR_005927). The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer; Greve & Fischl, 2009), resulting in a *preprocessed BOLD* image in T1w space.

After *fMRIPrep* preprocessing, masks generated for each BOLD scan were used to generate one mask based on the intersection of all masks. The first 10 frames (15s) of each *preprocessed BOLD* were discarded. Additionally, each *processed BOLD* was then scaled at a mean equal 100, with an upper bound of 200 and a lower bound of 0. Several confounding time-series were calculated based on the *preprocessed BOLD*: framewise displacement (FD), DVARS and three region-wise global signals. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (*CompCor*). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS were annotated as motion outliers. These were replaced by interpolating voxel values from neighboring data points using cubic spline interpolation (Brunec et al., 2018; Campbell et al., 2013; Thorp et al., 2022). This minimizes any effects of motion-induced spikes while also minimizing potential discontinuities in the fMRI time course due to the removal of outliers. The BOLD time-series were resampled into standard space, generating a *preprocessed BOLD* run in MNI152NLin2009cAsym space.

Region of interest (ROI) definition

To generate hippocampal ROIs, we used the Automatic Segmentation of Hippocampal Subfields (ASHS; Yushkevich et al., 2015) toolbox with the upenn2017 atlas. This generated subfield ROIs in each participant's hippocampal body: CA3/DG (which included CA3, CA2 and dentate gyrus) and CA1. The most anterior and posterior slices of the hippocampal body were manually determined for each participant based on the T2-weighted anatomical structure (Wanjia et al., 2021). Each participant's subfield segmentations were also manually inspected to ensure the accuracy of the segmentation protocol. Then, each subfield ROI was transformed into each participant's T1-weighted (T1w) space using the T2-to-T1w transformation, calculated with FLIRT (fsl) with six degrees of freedom, implemented with *Nipype*. Following the transformation to T1w space, all ROIs were again visually inspected to ensure that the ROIs were anatomically correct. Whole hippocampal masks were also extracted using FreeSurfer (Fischl, 2012). For each participant, the left and right hippocampal masks were combined and transformed into each participant's T1w space. Hippocampal masks were then split into anterior and posterior segments manually based on the T2-weighted anatomical structure, by using the position of the uncal apex as a conventional anatomical landmark (Poppenk et al., 2013). The anterior (aHPC) and posterior (pHPC) hippocampus ROIs were also visually inspected to ensure the ROIs were anatomically correct.

A region of interest (ROI) for early visual cortex (EVC) was derived from the probabilistic maps of Visual Topography (Wang et al., 2015) in MNI space, applying a threshold of 0.5. This ROI was then transformed into each participant's native space using inverse T1w-to-MNI nonlinear transformation. Following an approach used by Wanjia et al. (2021), an ROI for the parahippocampal place area (PPA) was created through an automated meta-analysis in Neurosynth using the key term "place". Clusters were then created based on voxels with a z-score greater than 2 from the Neurosynth associative tests. Next, we visually inspected the results, given that these clusters were generated through an automated meta-analysis and were not anatomically exclusive to PPA. The two largest clusters that were spatially consistent with PPA were manually selected: one was in the right hemisphere (voxel size = 247) and one in the left hemisphere (voxel size = 163). These clusters were combined into a single PPA mask. This mask was then transformed into each participant's native space using the inverse T1w-to-MNI transformation.

Additional ROIs for exploratory/control analyses were generated for the inferior frontal gyrus (IFG), entorhinal cortex (ERC), angular gyrus, and primary motor cortex (M1). These ROIs were extracted using anatomical labels defined by FreeSurfer's Desikan-Killiany atlas (Desikan et al., 2006). For IFG, the three subregions — pars opercularis, pars orbitalis, and pars triangularis — were combined into a single ROI. Bilateral ERC masks were created by combining left and right entorhinal labels. The same procedure was used to generate bilateral ROIs for the angular gyrus and M1. All ROIs were transformed into each participant's native T1-weighted space and visually inspected to ensure anatomical accuracy.

Autocorrelation analysis

Temporal autocorrelation was computed at the single voxel level (i.e., a separate autocorrelation value for each voxel), following procedures described by Bouffard and colleagues (2023). For all autocorrelation analyses, we used a lag of 1. Specifically, for each voxel within each ROI, the timeseries of activity from each encoding phase (i.e., excluding distractor and immediate recall phases) was temporally shifted by 1 TR (1500ms). Then, for each voxel, we calculated the Pearson correlation between the original timeseries and the temporally-shifted timeseries.

For analyses that compared autocorrelation across the switch rate conditions, we restricted the autocorrelation measure to timepoints (TRs) that followed the first context switch. Specifically, for the Low, Medium, and High Switch conditions, we selected the first timepoint (TR) that was at least 4s after the onset of the first context switch (range = 4-5s after context switch). The exact time windows used for the autocorrelation analyses for each switch rate condition were: Low Switch = 93s – 166.5s; Medium Switch = 54s – 166.5s; High Switch = 27s – 166.5s. Importantly, each of these autocorrelation windows was expressed relative to (or 'baselined' against) a corresponding window for the No Switch condition. For example, for the Low Switch condition, autocorrelation was computed for a window from 93s – 166.5s and this value was baselined against the exact same time window (93s – 166.5s) for the No Switch condition. Thus, the Low, Medium, and High switch conditions each had a unique baseline that was determined by subsampling the No Switch condition. Autocorrelation values were Fisher Z transformed and then averaged across voxels and across rounds, producing a single measure of autocorrelation per ROI, subject, and switch rate condition.

Correlation between temporal clustering and hippocampal autocorrelation

Lastly, we correlated temporal clustering scores with autocorrelation values separately for each ROI. In contrast to earlier analyses, autocorrelation was computed across the entire encoding phase—excluding distractor and recall periods—without restricting to timepoints following the first context switch. The rationale for using the entire encoding phase (instead of subsampling) was that temporal clustering scores reflect recall behavior from an entire study list and it is difficult to subsample temporal clustering. Thus, to align temporal clustering with autocorrelation, it makes the most sense to consider the full encoding phase for each measure. Moreover, here we were not interested in differences between conditions but instead in overall differences across participants. Autocorrelations values were Fisher Z-transformed, baseline-corrected using the No Switch condition, and averaged to yield one value per ROI, subject, and switch rate condition. Low and Medium Switch conditions were averaged to create a single Low/Medium condition for comparison to the High Switch condition. We ranked temporal clustering scores and autocorrelation values within each condition, averaged the ranks, and computed the Pearson correlation of these average ranked values. This analysis was motivated by parallel effects of switch rate on both temporal clustering and hippocampal autocorrelation.

Statistical tests

Statistical tests were conducted in R 4.2.3 (R Core Team 2020; https://www.R-project.org/). Behavioral and fMRI data were analyzed using a combination of paired *t* tests, repeated measures ANOVA, and Pearson correlations. Effect sizes (i.e., Cohen’s d and partial eta squared) were calculated using the *lsr* package in R. All t-tests were two-tailed unless otherwise noted. A threshold of $p < 0.05$ was used to establish statistical significance for all analyses.

Results

Behavioral measures of recall

During the encoding phases, participants indicated whether they could envision the referent of each word within the scene context. For trials on which participants made a response, the mean percentage of 'yes' responses was 19.77% ± 11.38% (s.d.). The percentage of ‘yes’ responses did not differ by switch rate condition (No Switch, Low, Medium, High; one-way repeated-measures ANOVA: $F_{2.77, 102.45} = 0.61$, $p = 0.60$, partial eta squared = .02).

During the immediate recall phases, participants attempted to recall as many words as possible from the immediately preceding study list. The mean percentage of words recalled was 38.51% ± 9.68%. A one-way repeated measures ANOVA did not yield a main effect of switch rate on the percentage of words recalled ($F_{2.68, 99.29} = 1.23$, $p = 0.30$, partial eta squared = .03; Figure 3.2a). The lack of an effect of context switch rate on overall recall is consistent with prior behavioral work (Rait et al., 2024).

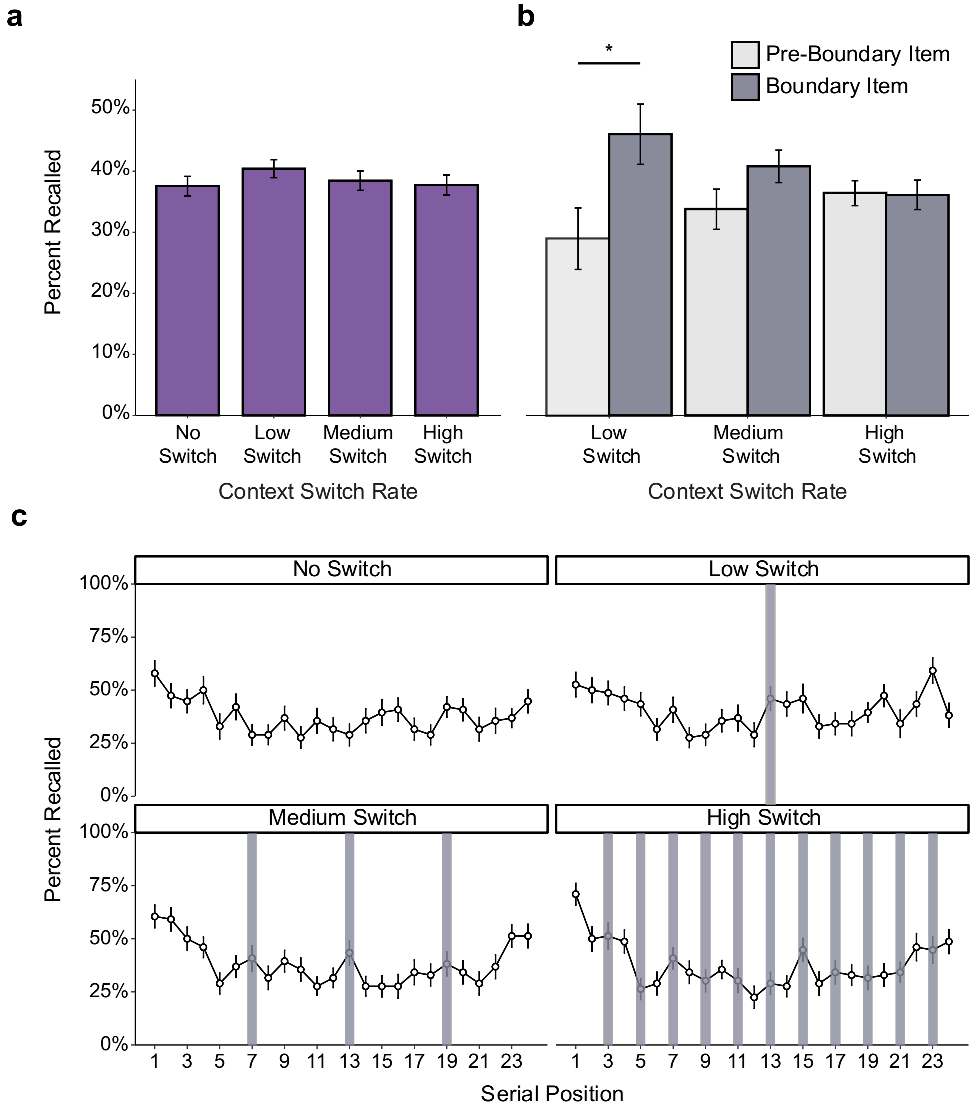

Figure 3.2. **Memory recall by condition and boundaries. a)** Percent of words recalled as a function of switch rate condition. There was no difference in the percent of words that participants recalled based on the switch rate condition (*p* = 0.30). **b)** Percent of words recalled as a function of switch rate condition and boundary status (boundary vs. pre-boundary). Participants recalled more boundary words than preboundary words only in the Low Switch condition (*p* = 0.026). **c)** Serial position curves for each switch rate condition. Shaded bars reflect boundary items. Note: error bars indicate ± SEM.

We next considered whether recall was influenced by context boundaries (i.e., changes in scene images). We defined *boundary items* as words that immediately followed a context change and *pre-boundary items* as words that immediately preceded a context change. Thus, because No Switch lists did not include any changes in context, there were no boundary or pre-boundary items in these lists. A repeated measures ANOVA with factors of context switch rate (Low, Medium, High) and boundary status (boundary vs. pre-boundary) revealed a significant main effect of boundary status ($F_{1,37} = 8.01$, $p = 0.007$, partial eta squared = 0.18), driven by a higher recall rate for boundary items than pre-boundary items (Figure 3.2b). The interaction between boundary status and context switch rate was not significant ($F_{1.38,51.15} = 2.99$, $p = 0.077$, partial eta squared = 0.07). However, post-hoc paired-samples t-tests revealed a significant advantage for boundary items vs. pre-boundary items only for the Low Switch condition (Low: $t_{37} = 2.32$, $p = 0.026$, $d = 0.38$; Medium: $t_{37} = 1.73$, $p = 0.092$, $d = 0.28$; High: $t_{37} = -0.14$, $p = 0.887$, $d = 0.02$). Figure 3.2c shows recall probability as a function of serial position, with boundary items highlighted in grey. While these boundary effects were not of primary interest in the current study, they do establish the important point that memory for the words was influenced by context changes.

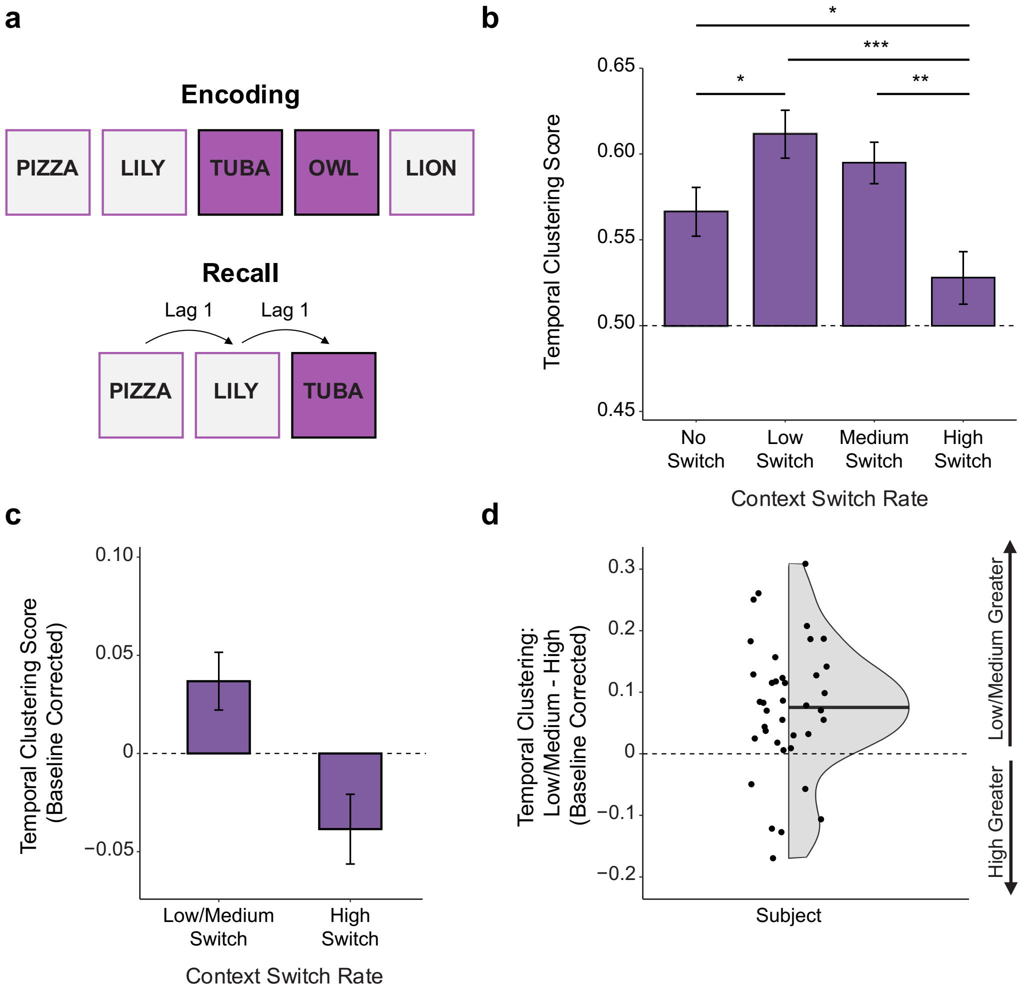

Figure 3.3. Temporal clustering during memory recall. **a)** Top: example subset of an encoding list with context changes reflected by a change in fill color. Bottom: example subset of a recall list demonstrating high temporal clustering (recall transitions preserve the temporal order from encoding). **b)** Temporal clustering scores as a function of switch rate condition. Temporal clustering in the High Switch condition was significantly lower than in the No Switch condition ($p = 0.036$), Low Switch condition ($p = 0.0003$), and Medium Switch condition ($p = 0.0009$). There was no difference in temporal clustering scores between the Low and Medium Switch conditions ($p = 0.377$). **c)** Baseline-corrected temporal clustering scores for the Low/Medium Switch and High Switch conditions (baseline = No Switch condition). **d)** Baseline-corrected temporal clustering scores for the Low/Medium Switch condition relative to the High Switch condition. Positive scores indicate greater temporal clustering in the Low/Medium Switch condition. Each dot represents an individual participant. Note: error bars indicate ± SEM.

Next—and of central interest—we tested whether context switch rate influenced the degree of temporal clustering of word recall (see Methods for description of how temporal clustering scores were computed). A one-way repeated-measures ANOVA with switch rate as a factor (No Switch, Low, Medium, High) revealed a significant main effect ($F_{2.88,106.57} = 7.83$, $p = 0.0001$, partial eta squared = .17) with temporal clustering numerically highest in the Low Switch condition and numerically lowest in the High Switch condition (Figure 3.3b). Follow-up paired-samples *t*-tests revealed that temporal clustering in the Low Switch condition was significantly greater than in the No Switch condition ($t_{37} = 2.53$, $p = 0.016$, $d = 0.41$) and High Switch condition ($t_{37} = 4.00$, $p = 0.0003$, $d = 0.65$), but did not differ from the Medium Switch condition ($t_{37} = 0.89$, $p = 0.377$, $d = 0.15$). Temporal clustering in the Medium Switch condition was significantly greater than in the High Switch condition ($t_{37} = 3.61$, $p = 0.0009$, $d = 0.59$), but did not differ from the No Switch condition ($t_{37} = 1.68$, $p = 0.102$, $d = 0.27$). Temporal clustering in the High Switch condition was significantly lower than in the No Switch condition ($t_{37} = -2.17$, $p = 0.036$, $d = 0.35$). Thus, while context switch rates did not influence the overall percentage of studied words that were recalled (Figure 3.2a), they had a substantial influence on the organization of recall. In particular—and consistent with our prediction—a relatively high context switch rate during encoding disrupted the degree of temporal clustering during recall.

Given the lack of a significant difference in temporal clustering for the Low vs. Medium Switch conditions (Figure 3.3b), for subsequent analyses (temporal clustering and fMRI) we combined (averaged) these two conditions into a single Low/Medium Switch condition. Additionally, in order to better isolate the effects of context switch rates, for all subsequent analyses (temporal clustering and fMRI) we used the No Switch condition as a participant-specific baseline that was subtracted from the Low/Medium (before averaging) and High Switch conditions. In other words, Low/Medium and High Switch conditions were expressed relative to the No Switch baseline. Figure 3.3c shows the reformatted data, clearly illustrating that temporal clustering in the Low/Medium Switch condition was higher than baseline, whereas temporal clustering in the High Switch condition was lower than baseline. The relative increase in temporal clustering in the Low/Medium Switch condition compared to the High Switch condition was evident in the majority of participants (Figure 3.3d).

fMRI measures of autocorrelation

All fMRI analyses focused on measures of autocorrelation: the degree to which fMRI activation at a given timepoint predicts activation at a subsequent timepoint. Based on leading theories which argue that the hippocampus plays a unique role in tracking context stability (Maurer & Nadel, 2021), we specifically predicted that context switch rate would influence autocorrelation values in the hippocampus.

To validate our measure of hippocampal autocorrelation, we first sought to replicate a previously-reported dissociation in autocorrelation along the long-axis of the hippocampus. Namely, prior studies have shown that autocorrelation values are higher in anterior (aHPC) compared to posterior (pHPC) hippocampus (Bouffard et al., 2023; Brunec et al., 2018). Averaging data across context switch rate conditions, we replicated this finding: autocorrelation values were higher in aHPC compared to pHPC (paired-samples *t*-test: $t_{37} = 2.37$, $p = 0.023$, $d = 0.38$; Figure 3.4b). Given our high-resolution imaging protocol, we also tested for differences between CA1 and CA3/DG—a comparison that, to our knowledge, has not previously been reported.

Interestingly, we found higher autocorrelation values in CA3/DG than CA1 ($t_{37} = 3.12$, $p = 0.004$, $d = 0.50$; Figure 3.4c).

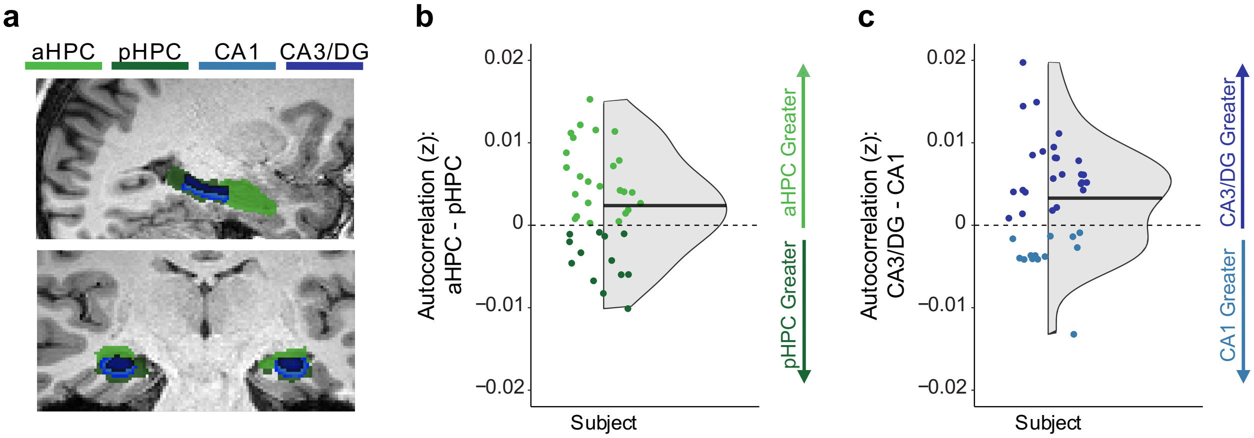

Figure 3.4. Temporal autocorrelation for hippocampal subregions. a) Hippocampal regions of interest (ROIs) included subregions based on the long-axis of the hippocampus, anterior hippocampus (aHPC, light green) and posterior hippocampus (pHPC, dark green), as well as hippocampal subfield CA1 (light blue) and hippocampal subfields CA3 and dentate gyrus (CA3/DG, dark blue) **b)** aHPC vs. pHPC. We found higher autocorrelation values in aHPC as compared to pHPC ($p = 0.023$). **c)** CA3/DG vs. CA1. We found higher autocorrelation values in CA3/DG as compared to CA1 ($p = 0.004$). Data in both graphs are averaged across context switch rate conditions.

Next, we addressed the critical question of whether context switch rate influenced autocorrelation values in the hippocampus. There were two important features of this analysis: (1) autocorrelation values for each switch rate condition were computed by subsampling the data from each encoding scan run to only include timepoints *after* the first context change, and (2) autocorrelation values for each switch rate condition were baselined against the No Switch condition using a matched subsampling (see Methods for details). The rationale for the subsampling (to only include timepoints after the first context change) was that there is no reason why autocorrelation values should differ *relative to the No Switch condition* before a context change has actually occurred.

Notably, we did not have an *a priori* prediction that the effect of context switch rate on autocorrelation would differ across hippocampal subregions. That said, given the overall differences in autocorrelation that we observed in the analyses reported above (Figure 3.4), we considered subregions as a factor in our analyses. We first tested for effects across the long-axis of the hippocampus. A two-way repeated measures ANOVA with factors of ROI (aHPC, pHPC) and context switch rate (Low/Medium, High) revealed a significant main effect of switch rate ($F_{1,37} = 5.25$, $p = 0.028$, partial eta squared = 0.12; Figure 3.5a), but no main effect of ROI ($F_{1,37} = 0.03$, $p = 0.854$, partial eta squared <0.001) and no interaction between switch rate and ROI ($F_{1,37} = 0.77$, $p = 0.385$, partial eta squared = 0.02). The main effect of switch rate reflected higher autocorrelation in the Low/Medium Switch condition relative to the High Switch condition. In other words, hippocampal activity patterns were relatively more stable when the context was more stable. Note: the lack of a main effect of ROI is not incongruent with the effects shown in Figure 3.4b because, here, autocorrelation values were baselined against the No Switch condition whereas the results in Figure 3.4b are averaged across all switch rate conditions (no baseline correction). Post-hoc paired samples t-tests indicated that autocorrelation in pHPC was significantly higher in the Low/Medium Switch condition compared to the High Switch condition ($t_{37} = 2.46$, $p = 0.018$, $d = 0.40$), with a qualitatively similar pattern in the aHPC ($t_{37} = 1.78$, $p = 0.084$, $d = 0.29$).

We next repeated the analysis above, but with CA1 and CA3/DG as the ROIs. Again, the main effect of switch rate was significant ($F_{1,37} = 5.83$, $p = 0.021$, partial eta squared = 0.14; Figure 3.5b), with no main effect of ROI ($F_{1,37} = 0.78$, $p = 0.384$, partial eta squared = 0.02) or interaction between ROI and switch rate ($F_{1,37} = 0.11$, $p = 0.737$, partial eta squared < 0.001). Thus, regardless of how we divided the hippocampus, we found that context switch rate influenced hippocampal autocorrelation. Again, the lack of a main effect of ROI is not incongruent with the effects shown in Figure 3.4c because, here, autocorrelation values were baselined against the No Switch condition whereas the results in Figure 3.4c are averaged across all switch rate conditions (no baseline correction). Post-hoc paired samples t-tests did not reveal significant differences between the Low/Medium and High Switch conditions for CA1 ($t_{37} = 1.80$, $p = 0.080$, $d = 0.29$) or CA3/DG ($t_{37} = 2.02$, $p = 0.051$, $d = 0.33$).

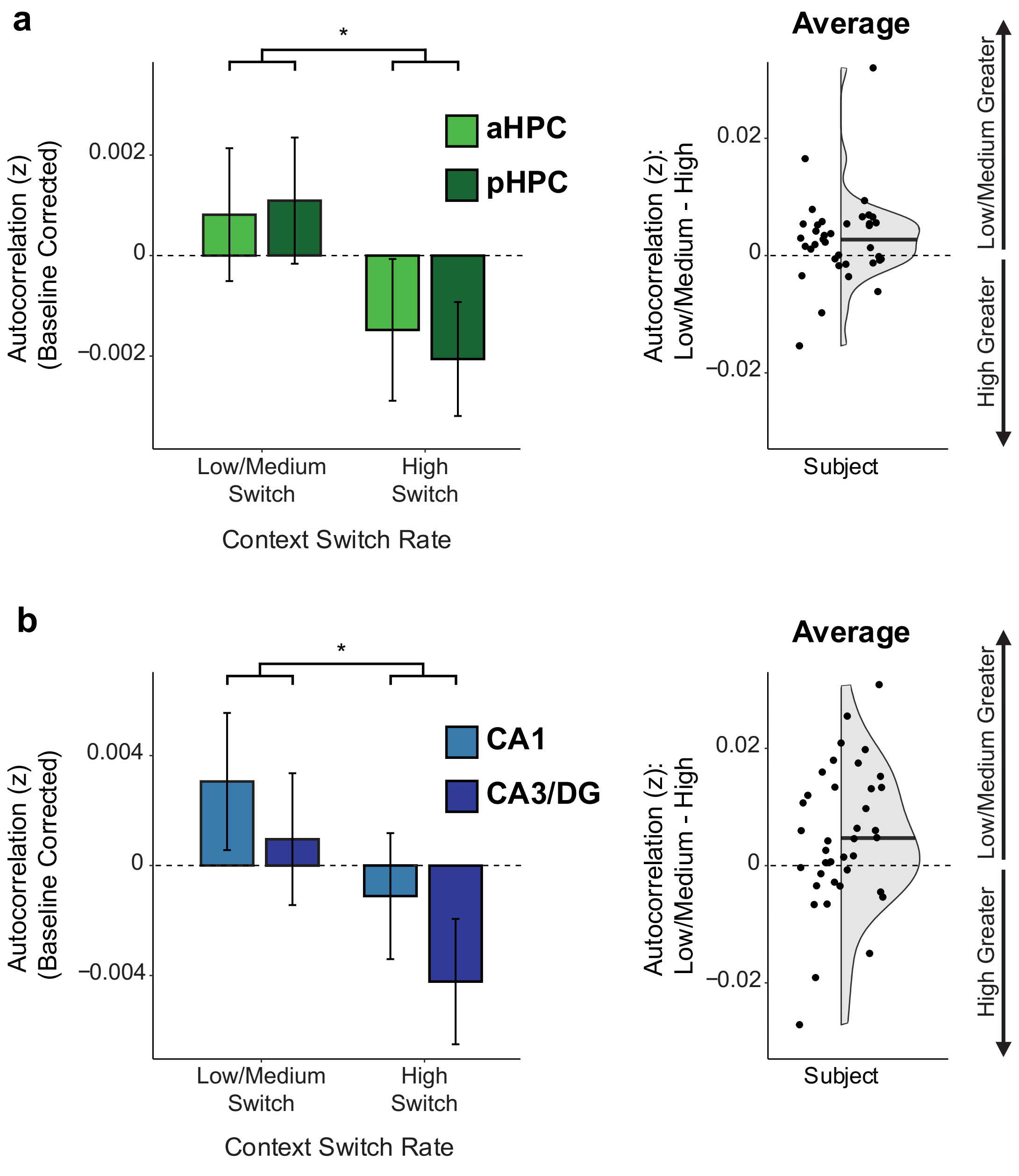

Figure 3.5. **Hippocampal autocorrelation as a function of switch rate condition.** **(a)** Left: autocorrelation in aHPC and pHPC revealed a significant main effect of switch rate condition ($p = 0.028$), reflecting higher autocorrelation in the Low/Medium Switch condition relative to the High Switch condition. Right: difference between Low/Medium vs. High Switch conditions, averaged across aHPC and pHPC; each dot represents an individual participant. **(b)** Autocorrelation CA1 and CA3/DG revealed a main effect of switch rate condition ($p = 0.021$), reflecting higher autocorrelation in the Low/Medium Switch condition relative to the High Switch

condition. Right: difference between Low/Medium vs. High Switch conditions, averaged across CA1 and CA3/DG; each dot represents an individual participant. Note: error bars indicate ± SEM.

Finally, we tested for effects of context switch rate (using paired-samples t-tests) in regions outside of the hippocampus. First, we tested a low-level visual cortical ROI (early visual cortex; EVC) and primary motor cortex (M1), two regions not typically implicated in context processing. As expected, there was no effect of context switch rate (Low/Medium vs. High) in EVC (t_{37} = -0.16, p =0.873, d = 0.03) or M1 (t_{37} = 1.27, p =0.207, d = 0.21) indicating that the effects in the hippocampus were not mirroring effects in early visual or motor regions. We next tested a high-level visual cortical ROI sensitive to scene information (parahippocampal place area; PPA). Given that the PPA is specifically sensitive to scene information, we expected it to show an effect of context switch rate similar to the hippocampus. Although the effect of context switch rate did not reach significance, the pattern of data was qualitatively similar to the posterior hippocampus (t_{37} = 1.98, p = 0.055, d = 0.32). Finally, we tested for effects within the angular gyrus, the inferior frontal gyrus (IFG), and entorhinal cortex (ERC). The rationale for considering the angular gyrus is that it has been implicated in long-timescale integration (Hasson et al., 2015). In contrast, IFG and ERC are regions previously shown to interact with the hippocampus to support temporal memory (DuBrow & Davachi, 2016; Zou et al., 2023). While the angular gyrus and IFG showed no effects of context switch rate (angular gyrus: t_{37} = 0.41, p =0.682, d = 0.07; IFG: t_{37} = 0.62, p =0.540, d = 0.10), autocorrelation in ERC was significantly higher in the Low/Medium Switch condition compared to the High Switch condition (t_{37} = 2.25, p =0.031, d = 0.36), mirroring effects in the hippocampus (Table 3.1). Together, these results highlight that the effect of context switch rate on autocorrelation was most pronounced in the hippocampus and ERC, regions that have each been associated with temporal memory.

Non-Hippocampal Regions of Interest	Effect of Switch Rate on Autocorrelation			Correlation with Temporal Clustering	
	t-value	*p*-value (two-tailed)	Cohen's *d*	*r*	*p*-value (one-tailed)
Early Visual Cortex (EVC)	-0.16	0.873	0.03	0.33	0.020
Parahippocampal Place Area (PPA)	1.98	0.055	0.32	0.12	0.241
Primary Motor Cortex (M1)	1.28	0.207	0.21	0.15	0.191
Angular Gyrus	0.41	0.682	0.07	0.04	0.403
Inferior Frontal Gyrus (IFG)	0.62	0.540	0.10	0.17	0.305
Entorhinal Cortex (ERC)	2.25	0.031	0.36	0.20	0.112

Table 3.1. Autocorrelation effects in non-hippocampal ROIs. Paired-samples *t*-tests compared autocorrelation values for the Low/Medium vs. High Switch conditions (positive *t* statistics indicate Low/Medium > High). Of the non-hippocampal ROIs considered, only the entorhinal cortex (ERC) showed a significant effect of switch rate on autocorrelation ($p = 0.031$). Across-participant correlations tested for relationships between autocorrelation and temporal clustering. Only early visual cortex (EVC) showed a significant correlation between autocorrelation and temporal clustering.

Relationship between hippocampal autocorrelation and temporal clustering in recall

Taken together, the behavioral and fMRI results described above indicate that context switch rate had parallel effects on temporal clustering and on hippocampal autocorrelation. Specifically, a high switch rate was associated with lower temporal clustering of recall and lower autocorrelation in the hippocampus. In a final set of analyses, we tested for a direct relationship between these measures using across-participant correlations. Notably, whereas the autocorrelation analyses reported above subsampled data from each encoding phase run to only include timepoints after the first context switch occurred, here no subsampling was applied (see Methods for rationale). Additionally, in order to obtain a single temporal clustering score per participant and a single autocorrelation score per participant, we averaged data across the Low/Medium and High Switch conditions (see Methods for details). Importantly, however, the temporal clustering and autocorrelation values were still baselined against the No Switch condition, as in the preceding analyses, to control for global effects. All correlations (Pearson r) were performed on the ranks of temporal clustering and autocorrelation values in order to minimize the influence of extreme values.

Because context switch rate had similar effects on temporal clustering and hippocampal autocorrelation *within participants*, we predicted a positive correlation between these variables *across participants*—i.e., that participants that exhibited higher hippocampal autocorrelation would also exhibit higher temporal clustering. Given this clear *a priori* prediction, we used one-tailed tests. First, considering ROIs segmented based on the long-axis of the hippocampus, positive correlations between autocorrelation and temporal clustering were observed for aHPC ($r(36) = 0.27$, $p = 0.049$) and pHPC ($r(36) = 0.27$, $p = 0.048$; Figure 3.6a). Next, considering hippocampal subfields, a positive correlation was observed for CA3/DG ($r(36) = 0.39$, $p = 0.008$) but not CA1 ($r(36) = -0.17$, $p = 0.845$; Figure 3.6b). There was also a significant difference between the strength of correlations in CA1 vs. CA3/DG ($z = 2.43$, $p = 0.015$; two-tailed). These findings establish a direct link between the stability of activity patterns in the hippocampus during encoding and the degree of temporal clustering during subsequent free recall.

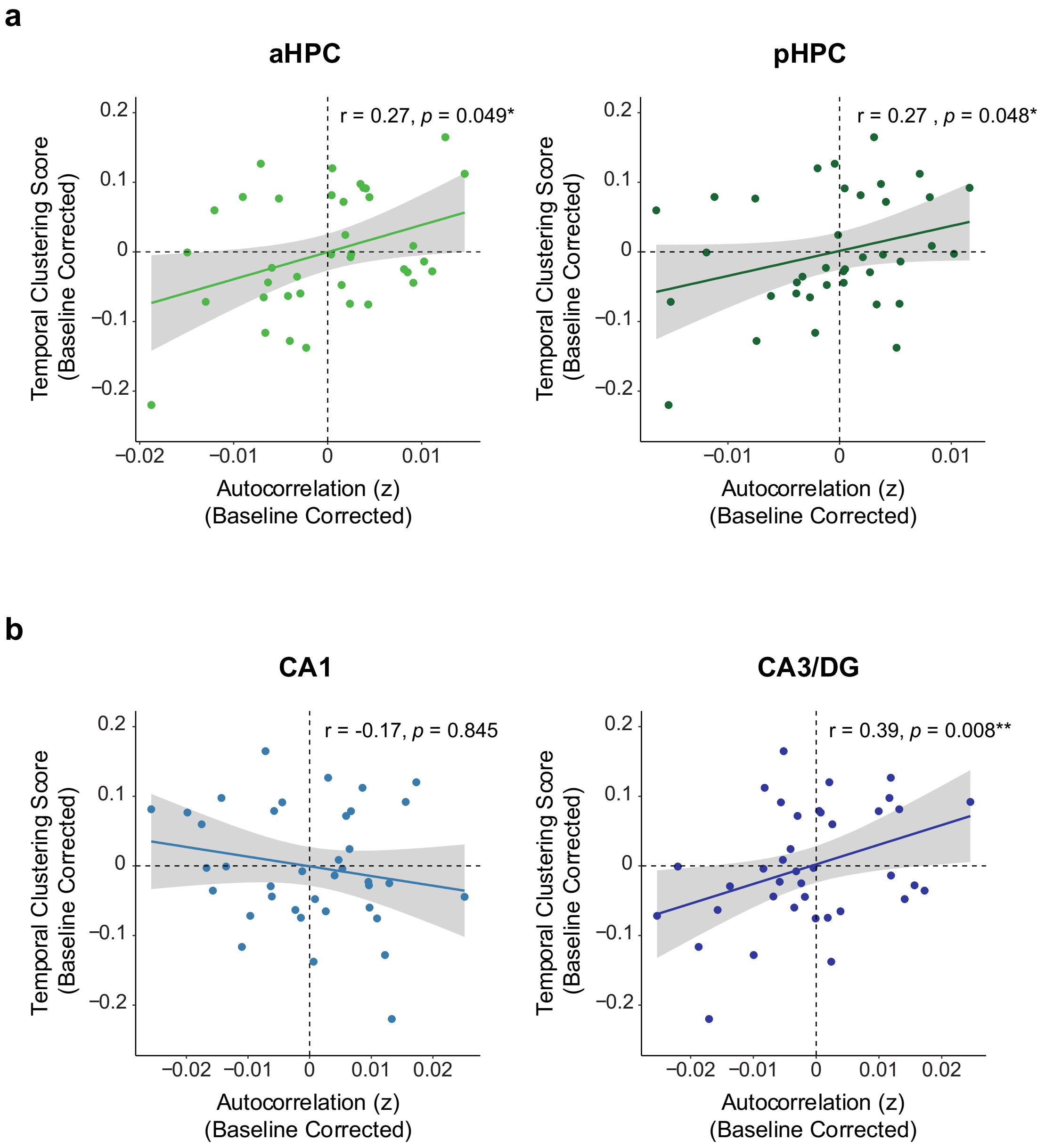

Figure 3.6. Relationship between hippocampal autocorrelation (during memory encoding) and temporal clustering (during subsequent recall). a) For anterior hippocampus (aHPC; left) and posterior hippocampus (pHPC; right), there were significant, positive correlations (one-tailed) between autocorrelation and temporal clustering (*p*'s < .05). **b)** For CA1, the correlation between autocorrelation and temporal clustering was not significant. For CA3/DG, there was a significant, positive correlation (one-tailed) between autocorrelation and temporal clustering ($p = 0.008$). The correlations in CA1 and CA3/DG were also significantly different from each other ($p = 0.015$). Note: all correlations were performed across participants; each dot represents data from an individual participant.

Discussion

Here, using a free recall paradigm in which we manipulated the rate of context change during encoding, we establish important links between memory organization (measured by temporal clustering) and drift rate within the hippocampus (measured by autocorrelation). While context switch rate had no effect on the total number of words recalled, it powerfully influenced the degree of temporal clustering during recall. Specifically, a higher context switch rate was associated with relatively less temporal clustering. This pattern of data was mirrored by autocorrelation in the hippocampus: a higher context switch rate resulted in relatively lower hippocampal autocorrelation. Finally, collapsing across the context switch rate conditions, we showed that participants that exhibited greater hippocampal autocorrelation during encoding also exhibited stronger temporal clustering during free recall.

A key feature of our experimental approach was that we actively manipulated the *rate* at which context (scene images) changed. While the scene images were not explicitly relevant to participants' goals during free recall, our behavioral results clearly demonstrate that changes in scene context had influenced multiple aspects of recall. First, we found that memory was enhanced (higher recall probability) for items that followed a context shift. This aligns with prior research showing that events that follow an external context change (a boundary) are better remembered (Jeunehomme & D'Argembeau, 2020; Polyn et al., 2009b). However, there are also several examples where boundary-related memory benefits have not been observed in free recall (Gold et al., 2017; Heusser et al., 2018; Pettijohn et al., 2016), suggesting that there are constraints on when boundaries enhance memory. Here, we replicate prior work (Rait et al., 2024) showing that boundary enhancement effects are eliminated when context changes occurred frequently (i.e., in the High Switch condition). This finding provides an important demonstration that the effect of context change on memory depends on the *rate* at which context is changing. Our interpretation of why rapid context changes diminished boundary enhancement effects is that when context shifts occur frequently, elements of the prior context persist and overlap with the new context, creating a “blended” representation (Polyn et al., 2012; Rait et al., 2024). When this occurs, boundaries may no longer stand out as discrete or novel events, reducing their salience and weakening the attentional orienting response typically observed at event transitions (Clewett et al., 2019; Zacks & Swallow, 2007). As a result, the memory advantage typically observed for boundary items is diminished.

Second, and of central interest in the present study, we found that context switch rate robustly influenced temporal clustering. Our focus on temporal clustering as a behavioral expression of memory organization was motivated by an extensive literature documenting and characterizing temporal clustering effects in free recall (Farrell, 2012; Kahana, 1996; Sederberg et al., 2010). In particular, temporal clustering has served as a primary inspiration for theories suggesting that internal context representations drift slowly across time (Howard & Kahana, 2002; Polyn et al., 2009a; Sederberg et al., 2008). Previous research has demonstrated that temporal clustering is robust across a variety of task parameters, such as the insertion of an effortful distraction task, (Healey et al., 2019; Howard & Kahana, 1999, 2002; Sederberg et al., 2008), suggesting that it is a stable feature of memory organization. However, more recent studies have highlighted that specific task and stimuli manipulations can have a surprisingly strong impact on temporal clustering (Hong et al., 2024; Manning et al., 2023). Here, we show that the High Switch condition was associated with less temporal clustering than the No Switch condition, suggesting that frequent switches actively disrupted temporal context representations. This finding is consistent with prior evidence and arguments that changes in context reset temporal context representations (Pu et al., 2022). Interestingly the Low/Medium Switch condition was associated with *more* temporal clustering than the No Switch condition. We interpret this as an interaction between temporal clustering and clustering based on the scene category ('source clustering'). Namely, a single context shift (change in scene category) halfway through the study list may have potentiated the salience of the category change, thereby increasing the tendency for participants to organize their memories according to the scene context (source clustering). Source clustering would, in turn, encourage relatively local recall transitions (within each half of the study list). In contrast, in the No Switch condition, any source clustering (by category) would occur across the *entire list* and, therefore, would not produce local recall transitions. Thus, our manipulation of context switch rate potentially resulted in tradeoffs between temporal vs. source clustering; however, our rationale for focusing on temporal clustering was that hippocampal drift is more naturally related to temporal organization than source organization.

Our prediction that context switch rate would specifically influence autocorrelation in the hippocampus was motivated by the widely accepted idea that the hippocampus is involved in memory for an event's context (Davachi, 2006; Eichenbaum et al., 2012; Maren et al., 2013; Ranganath, 2010a, 2010b; Rudy, 2009; Smith & Mizumori, 2006). In particular, empirical evidence and theories argue that time-varying changes in hippocampal activity patterns (drift) provide a basis for temporal context representations (Folkerts et al., 2018; Manns et al., 2007). While prior work has demonstrated slow, gradual drift in hippocampal activity over time, internal context representations are also thought to shift abruptly in response to salient changes in the external environment (DuBrow et al., 2017). Indeed, multiple studies have demonstrated that the hippocampus is sensitive to external context changes (Baldassano et al., 2017; Ben-Yakov et al., 2013; Ben-Yakov & Dudai, 2011; Ben-Yakov & Henson, 2018; Reagh et al., 2020; Yoo et al., 2021; Zheng et al., 2022). Building on this work, we show that the *rate* of these external context changes influences the *rate* of hippocampal drift. This finding validates computational models of memory, which propose that shifts in task context accelerate the rate of temporal context updating (Polyn et al., 2009a, 2012).

Our findings also add to a growing body of evidence that implicates the hippocampus in processing and remembering temporal information (Davachi & DuBrow, 2015; Eichenbaum, 2014; Polyn & Cutler, 2017; Zou et al., 2023). In particular, intact hippocampal function has been shown to be critical for the temporal organization of memory, with studies linking hippocampal activity to temporal clustering during free recall (Goyal et al., 2018; Long & Kahana, 2015). Previous research using invasive recordings in humans has suggested that gradually drifting activity in the temporal lobe supports associations between temporally adjacent items (El-Kalliny et al., 2019; Manning et al., 2011). Importantly, evidence from fMRI studies showed that the degree of drift specifically in the hippocampus predicts subsequent temporal memory judgments (DuBrow & Davachi, 2014; Ezzyat & Davachi, 2014; Jenkins & Ranganath, 2016). This relationship has also been observed in free recall, where hippocampal firing rate stability during encoding (Umbach et al., 2020) and the magnitude of reinstatement at retrieval (Yoo et al., 2021) are both linked to greater temporal clustering. However, recent evidence showed that event boundaries led to abrupt changes in medial temporal lobe (MTL) activity, which was associated with impairments in temporal order memory (Zheng et al., 2022). These findings suggest that disrupting gradual, continuous changes in MTL activity over time can interfere with the temporal organization of memory. Building on this work, the present study demonstrates that externally driven context shifts can modulate the rate of hippocampal drift and lead to corresponding changes in temporal clustering during recall, establishing a direct link between context dynamics, hippocampal stability, and recall organization.

Our fMRI findings additionally contribute to a growing body of evidence supporting functional specialization along the hippocampal long axis in both humans (Poppenk et al 2013; Brunec et al., 2018; Bouffard et al., 2023; Thorp et al.) and rodents (Fanselow & Dong, 2010, Moser & Moser, 1998, Komorowski et al 2013). Specifically, prior research in humans has shown that the anterior hippocampus (aHPC) maintains coarser-grained representations, characterized by more stable and slowly drifting signals over time, compared to the posterior hippocampus (pHPC; Bouffard et al., 2023; Brunec et al., 2018). Our results align with this gradient along the hippocampal long-axis and reveal a novel distinction in the rate of hippocampal drift within hippocampal subfields, with higher autocorrelation in CA3/DG than CA1. Interestingly, while we observed overall differences in autocorrelation across both the hippocampal long axis (aHPC vs. pHPC) and subfields (CA1 vs. CA3/DG), the effect of context switch rate was not statistically distinct in these regions. This suggests that while hippocampal drift varies across subregions, its sensitivity to externally driven context shifts may be more uniform. However, we did find that the across-participant relationship between autocorrelation and temporal clustering was stronger in CA3/DG than in CA1. Given that this was not a dissociation we predicted in advance, it will be of interest in future research to test whether drift rate in CA3/DG vs. CA1 is differentially predictive of temporal clustering.

In conclusion, our findings provide unique evidence that drift rate within the hippocampus is linked to the rate of context change and to the temporal organization of free recall. These findings support and extend influential computational models which describe how context shapes memory (Howard & Kahana, 2002; Polyn et al., 2009a).

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CHAPTER IV

AGENCY ALTERS MEMORY ORGANIZATION DURING FREE RECALL

This chapter is submitted for publication by Lindsay I. Rait, Elizabeth A. Horwath, Sarah DuBrow, and Vishnu P. Murty

Introduction

Individuals value the ability to exert agency and actively make choices that further shape their experiences (Code, 2020; Haggard, 2017; Haggard & Chambon, 2012; Leotti et al., 2010; Martin, 2004). While prior research indicated that exerting agency can increase the value of choice outcomes (Izuma & Murayama, 2013), more recent research demonstrated that making choices can also influence what is remembered (DuBrow et al., 2019; Gureckis & Markant, 2012; Hon & Yeo, 2021; Markant et al., 2014; Murty et al., 2015, 2019; Rotem-Turchinski et al., 2019). Expanding on this, prior work from our lab (Ruiz et al., 2023a) found that when participants had agency over making decisions, they exhibited stronger associative links in memory between decision cues, the decisions they made, and the outcomes using alternative forced choice paradigms. This suggests that agency not only affects what is remembered, but also how different pieces of information become connected in memory. However, in this paradigm, participants were explicitly instructed to make judgements about sequence information, precluding the ability to look at how agency influences the implicit organization of memory. Therefore, it is currently unknown whether agency influences the order in which items are remembered—or how memories are organized.

To explore memory organization more broadly, in the current study we used a free recall paradigm, which allows individuals to retrieve studied information without explicit cues about recall order, providing a unique window into the structure of natural memory (Rait & Hutchinson, 2024). Leading theoretical accounts propose that recall order is guided by the similarity of encoding contexts, with items encoded in similar contexts more likely to be recalled successively (Howard & Kahana, 2002; Polyn et al., 2009a; Sederberg et al., 2008). Because temporally adjacent items are often experienced in similar contexts, these shared contextual features (i.e., temporal context) serve as cues during retrieval. This makes it more likely that people recall items in the original study order—a pattern known as temporal clustering (Kahana, 1996; Sederberg et al., 2010). While agency has been shown to enhance memory for temporal order during exploration (Houser et al., 2022), it remains unclear whether this translates to free recall. In fact, prior research from our lab found no differences in temporal clustering based on motivational context, suggesting that alternative organizational strategies may take precedence over temporal order in certain situations (Horwath et al., 2023, 2024).

Context shifts (e.g., changes in location, task demands, or goal states) have been shown to disrupt temporal context (DuBrow et al., 2017; Lohnas et al., 2023; Polyn et al., 2009a; Pu et al., 2022). In these situations, individuals tend to organize memories around the new context, grouping together items from the same task (Polyn et al., 2009b). Prior research has shown that motivational factors, such as reward value, shape memory organization by promoting the grouping of information based on higher-order categories (Horwath et al., 2023). However, it is less clear whether this same effect holds in the context of agency, which engages similar neural circuitry but is not explicitly associated with reward incentives (Murty et al., 2015). When individuals are given the ability to make choices, they may prioritize organizing their memories based on the relationships established through those choices—even if those choices are not consequential—rather than on temporal proximity. Thus, we hypothesize that participants with agency over their choices will group items in memory based on the choices they actively made during encoding.

In the present study, we examined how imbuing individuals with agency during decision-making affects the later organization of memories in a between-groups design. Participants encoded lists of items while either actively making choices (Choice group) or following a yoked partner's choices (Fixed group). We measured recall organization to determine how agency influences the extent to which items are organized by the order in which they were encoded compared to the relationships they constructed through their choices. This design allowed us to ask whether and how the presence of agency alters the underlying structure of memory.

Methods

Participants

One hundred and thirty-two participants from the University of Oregon completed this experiment online for course credit. Eight participants were excluded for failing to provide audio usable for verbal recall, four participants were excluded for writing down words as indicated on a post-experiment questionnaire, and 20 participants were excluded for not following instructions correctly. Given that this is a yoked design, the 32 yoked partners of these participants were also removed. The final sample size for analysis was 68 participants (43 female, mean age 20.10 ± 5.50 s.d.). Data was collected in three separate batches. The Choice group (n = 34) was collected first in each batch. Their responses were later shown to yoked partners in the Fixed group (n= 34).

Consent was obtained in a manner approved by University of Oregon’s Institutional Review Board.

Stimuli

The experiment consisted of 20 unique cartoon figures generated within the Toca Boca application (https:// tocaboca.com/apps). The Toca Boca characters have been used in previous studies in our lab (Murty et al., 2020; Ruiz et al., 2023b), and all contained neutral facial expressions. All characters were also given a gender-neutral name written above the character. Toca Boca characters were put into 10 pairs of two characters. Words were 100 two-syllable nouns presented in capitalized letters (e.g., “EARRING”) that were based on object image labels from the Bank of Standardized Stimuli (Brodeur et al., 2014). To generate the final word list, latent semantic analysis (cutoff of .5) was used to ensure that none of the words were too similar to each other or to a one-word description of each Toca Boca character (e.g., “Butterfly”) that we generated. These choices were made to ensure that nothing about the words or the characters themselves could influence participant choices. Presentation order of character pairs and order of the words were randomized for each subject in the Choice group. Also, for participants in the Choice group, which character appeared on the left versus the right side of the screen was counterbalanced across participants. Stimuli were presented using Inquisit 6 [computer software]. (2020). Retrieved from https://www.millisecond.com.

Experimental procedure

The experiment consisted of 10 lists, with each list consisting of three sequential phases: encoding, distractor, and recall. During encoding, participants were instructed to create meaningful gift baskets for two characters displayed in the center of the screen, with their names labeled above them. The item to be sorted, presented as a word in all capital letters, appeared below the characters. Ten empty circles, five next to each character, were displayed help participants evenly distribute items. On each trial, participants in the Choice group had 4,000ms to decide which character would receive the item, responding via the keyboard ("z" for the character on the left and "m" for the character on the right). Participants were instructed to assign five items to each character across the 10 trials. Critically, participants received no instructions about how to assign items, and the characters themselves offered no inherent cues about how the items should be grouped. Therefore, any meaning assigned to the characters or organization of the items was entirely generated by the participant. To help track this, the corresponding circle next to the chosen character and their name turned blue upon selection (Figure 4.1, top**).** In contrast, participants in the Fixed group were guided by a visual cue—a rectangle around the character's name-— indicating which character should receive the item (Figure 4.1, bottom). This instruction was based on the previous choices made by a yoked participant in the Choice group. Even though participants in the Fixed group could not choose which character should receive the item, they were still required to make a keypress to give the item to the corresponding character based on the cue. For both groups, all stimuli remained on the screen for the full 4,000ms regardless of response time in order to ensure equal encoding duration across trials and groups. Additionally, each list featured a different pair of Toca Boca characters.

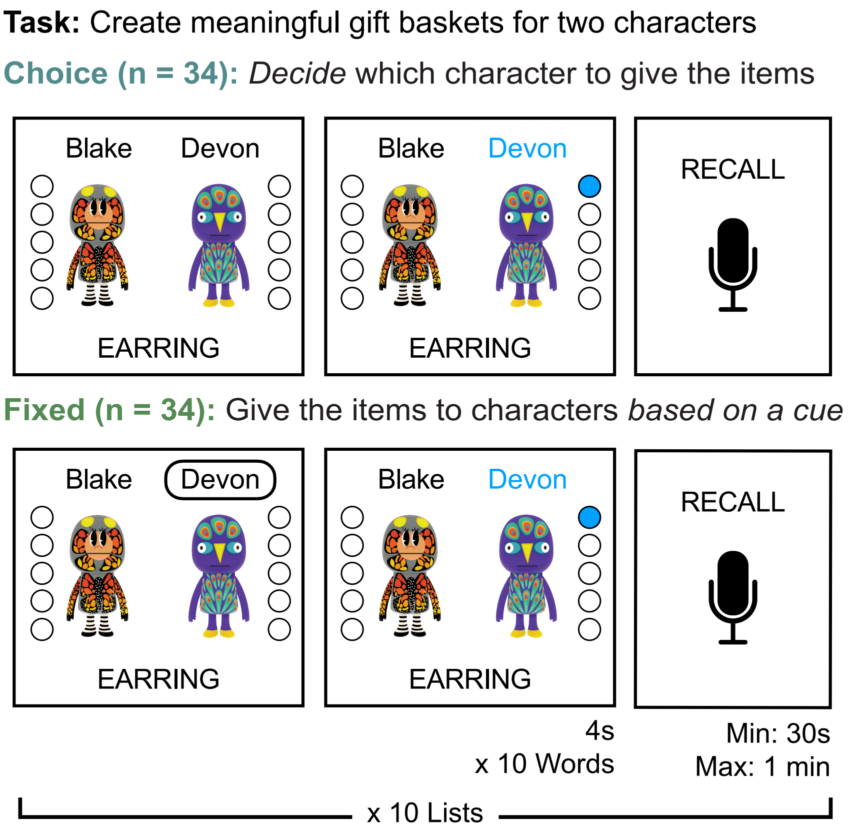

Figure 4.1. Experimental design. On each trial, participants assigned an item (word) to one of two characters in order to create meaningful gift baskets for each character (“z” for the character on the left and “m” for the character on the right). In the Choice group (top), participants decided the recipient within 4,000ms, and received feedback to track the number of items sorted for each character to ensure even division. Critically, participants received no instructions about how to assign items, and the characters themselves offered no inherent cues about how the items should be grouped. In the Fixed group (bottom), a rectangle around the character’s name indicated the assigned recipient, based on the choices of a yoked participant from the Choice group. Each list contained 10 items and featured different character pairs. After each list, participants verbally recalled as many items as possible for a maximum of one minute.

Immediately following each encoding phase, participants completed a math distractor task to reduce rehearsal. Participants were presented with math equations in the form of A + B + C = D, where the values of A, B, and C were set to single digit integers (Howard & Kahana, 1999).

Participants were instructed to indicate whether the statement was true or false with a key press. The distractor phase lasted 10s in total, but the number of equations completed was variable depending on speed of completion.

After the distractor task, participants were given one minute to verbally recall as many words as possible from the list that they could, without any explicit instructions about the order of the of recall. Participants saw the word "RECALL" appear on the screen, which indicated the start of the recall period. Their responses were recorded via a microphone on their computer that was only turned on for recording during the free recall portion of the experiment.

Data analysis

Statistical analyses were conducted in R 4.2.3 (R Core Team 2020; https://www.R-project.org/). During encoding, participants in the Choice group could choose which character to give the item to. We calculated the probability that, after making a response, the next item was given to the same character (stay) versus a different character (switch). This analysis could not be conducted for the Fixed group, as their responses were yoked to those in the Choice group. To quantify this behavior, we calculated a 'stay choice' score by dividing the number of times a participant chose the same character on consecutive trials by the total number of choices made (always 9, since the first choice on each list is excluded since it has no prior choice to compare).

A one-sample t-test was conducted to determine whether participants in the Choice group were more likely to switch than stay. Additionally, we calculated the maximum number of switch choices that were made for each list to later compare to memory performance (as difference scores). To do this, we calculated the longest streak of consecutive switch choices during encoding—instances where a participant changed their assignment of items between characters—within each list.

We measured free recall accuracy on a word-level basis by determining whether each encoded word was recalled. A mixed-effects logistic regression model (*glmer* function from the *lme4* package) was used to determine whether group (Choice vs. Fixed) predicted the likelihood of recalling a given word. The binary outcome variable was whether or not a given item was recalled on a given trial (1 = word recalled, 0 = word not recalled). A yoked pair subject identifier (e.g., Pair A = Subjects 1 & 2) was assigned to pairs of participants who were matched across groups to account for shared variance between yoked participants. Yoked pair subject and word identity were included as random effects. List number was included as a fixed effect to control for potential list-related variation. We used multilevel models in order to account for subject-level differences in the effect of choice on memory and differences in memorability across encoded words.

Verbal recall responses were digitally recorded and annotated offline using Penn Total Recall (http://memory.psych.upenn.edu/TotalRecall). Two undergraduate research assistants, who were blind to which participants were randomly assigned to which group, transcribed the verbal responses. A recall was classified as valid if the item recalled was present in the current list. Words from previous lists, words not in the wordpool, or other vocalizations (e.g, "umm") were not included in analysis.

Temporal clustering analysis

We investigated how having a choice influenced the order in which items were recalled from memory, as measured by the degree of temporal clustering in recall. Temporal clustering is the tendency to successively recall items that were encoded in nearby positions on the study list. We calculated a temporal clustering score for each participant in each group for each of the 10 lists (Polyn et al., 2009a). To measure temporal clustering, we determined the temporal distance (in absolute lag) between the just-recalled word and the next word actually recalled, as well as the distances between the just-recalled word and all words not yet recalled (possible lags) for every recall transition. Next, we compared the actual lag to the set of possible lags. The temporal clustering score is calculated as the proportion of possible lags greater than the actual lag. A score of 1 indicates high temporal clustering, meaning that participants recalled items in the exact order (or reverse order) they were studied, making the shortest possible transitions between recalled items. A score of 0.5 indicates chance-level temporal clustering, meaning that transitions were just as likely to be to a nearby or remote item. Temporal clustering scores were computed using publicly available MATLAB (The MathWorks, Natick, MA) scripts from the Behavioral Toolbox (Version 1.01) from the Computational Memory Lab (http://memory.psych.upenn.edu/Behavioral_toolbox).

Using the *lme4* package in R, we fit a linear mixed-effects model to examine whether group (Choice vs. Fixed) predicted the amount of temporal clustering on a given list, with yoked pair subject identity as a random effect. This model also included the percent of words recalled (calculated separately for each participant in each group for each of the 10 lists) and list number as fixed effects.

Decision clustering analysis

We next investigated the extent to which participants successively recalled items that were given to the same character. To calculate decision clustering, we used a method previously used by our group (Horwath et al., 2023). We separately calculated the proportion of recall transitions that stayed within the same character (e.g., Devon to Devon, or Blake to Blake) versus the number of transitions that switched between characters (e.g., Devon to Blake, or Blake to Devon). The transition probability score is determined by subtracting the real and chance probabilities for a given subject. To calculate the real transition probabilities, we computed the number of stay (or switch) transitions and divided that by the total number of transitions made. Then, for each transition, we determined the chance of staying with the same (or switching to the other) character by calculating the total number of recalled words remaining from each character and dividing that by the total number of transitions remaining. This allows for a dynamic, idiosyncratic level of chance performance for each participant.

Using the *lme4* package in R, a linear mixed-effects model was used to determine whether group (Choice vs. Fixed) predicted the proportion of transitions that stayed within the same character on a given list, with yoked pair subject identity as a random effect. A separate model was used to determine whether group (Choice vs. Fixed) predicted the proportion of transitions that switch to the other character on a given list, with yoked pair subject identity as a random effect. Both models also controlled for the percent of words recalled (calculated separately for each participant in each group for each of the 10 lists) and list number as fixed effects.

Results

We first examined the order in which participants in the Choice group assigned items to the two characters at encoding. A one-sample t-test revealed that the probability of switching characters (e.g., Blake to Devon) during encoding was significantly greater than 50%, (M = 67.19% ± 10.61%, s.d.), $t(33) = 9.45$, $p < 0.001$, indicating a systematic bias toward switching characters.

Next, to characterize how agency influenced overall recall performance, we compared the number of items recalled from the immediately preceding study list between the Choice and Fixed groups. Across both groups, the mean recall was 48.68% ± 11.43%. We then ran a mixed-effects logistic regression model predicting word recall (yes/no) by group (Choice vs. Fixed), also including a fixed effect of list number and random effects of word and yoked pair subject identity. The analysis showed that group did not significantly predict recall performance ($\beta = -0.03$, $p = 0.55$, 95% CI [-0.13, 0.07]), suggesting that the likelihood of recalling a word is not influenced by whether participants have agency over their choices.

Next—and of central interest—we investigated whether making a choice, rather than having it made for you, influenced memory organization. We first investigated this through temporal clustering, the tendency to successively recall items (recall transition) encoded in nearby positions on the study list. We calculated a temporal clustering score for each participant in each group for each list (Polyn et al., 2009a). A score of 1 indicates high temporal clustering, meaning that participants recalled items in the exact order (or reverse order) they were studied. A score of 0.5 indicates chance-level temporal clustering, meaning that transitions were just as likely to be to a nearby or remote item (see Methods). While temporal clustering was above that expected by chance in both groups (clustering scores > .5; Choice: $t(33) = 6.28$, $p < 0.001$; Fixed: $t(33) = 8.69$, $p < 0.001$, one-sample t-tests), group significantly predicted temporal clustering scores ($\beta = 0.04$, $p = 0.012$, 95% CI [0.01, 0.07]; linear mixed-effects regression model; Figure 4.2), such that temporal clustering was significantly lower in the Choice compared to Fixed group (see Table S4.1 for full model details). When participants had no control over their choices, they relied more on the original study order to structure their recall. In contrast, participants with agency may have used alternative organizational strategies, reducing their dependence on temporal structure.

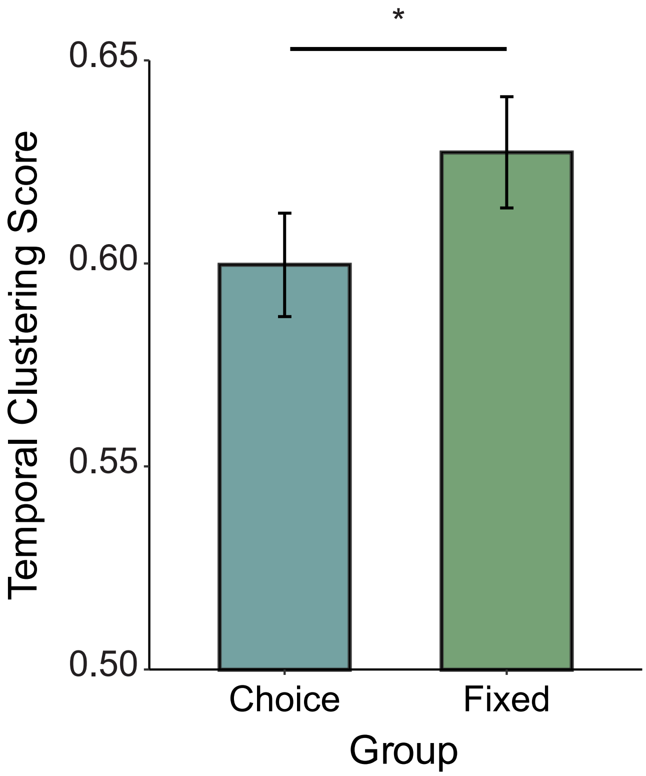

Figure 4.2. Temporal clustering by group. Participants in the Fixed group had significantly higher temporal clustering scores than participants in the Choice group. * $p < .05$. Error bars indicate ± SEM.

To further explore the organizational strategies of participants in the Choice group, we characterized whether making choices during encoding could serve as a context that later organizes memory. To test this, we examined whether participants were more likely to successively recall items that had been given to the same character. We separately calculated the proportion of recall transitions that stayed within the same character (e.g., Devon to Devon) versus the number of transitions that switched between characters (e.g., Devon to Blake; see Methods and Horwath et al., 2023 for details) for each participant in each group for each list. We found that group significantly predicted stay transition probabilities (β = -0.05, p = 0.024, 95% CI [-0.10, -0.007]; linear mixed-effects regression model; Figure 4.3a), with participants in the Choice group making more within-character transitions than those in the Fixed group (see Table S4.2 for full model details). This suggests that when a participant in the Choice group recalled a word, they were more likely to recall their next word as one that had been assigned to the same character. In contrast, group was not a significant predictor of switch transition probabilities (β = -0.003, p = 0.924, 95% CI [-0.07, 0.07]; Figure 4.3b), meaning that the groups did not differ in how often they transition between characters during recall.

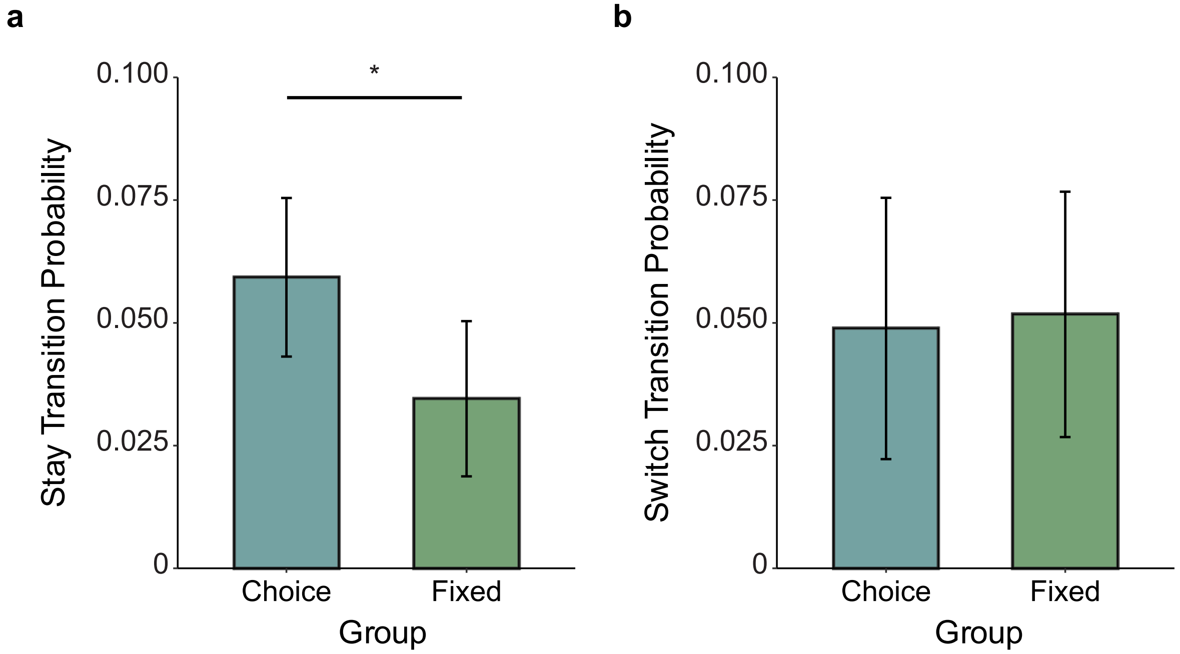

Figure 4.3. Decision clustering. a) Stay transition probability by group. We calculated the proportion of recall transitions that stayed within the same character. Participants in the Choice group made significantly more stay transitions than participants in the Fixed group. **b)** Switch transition probability by group. We calculated the proportion of recall transitions that switched between the two characters. There was no difference in the number of switch transitions made between participants in the Choice and Fixed groups. * $p < .05$. Error bars indicate ± SEM.

Lastly, we examined whether the pattern of encoding choices was related to subsequent recall performance. To quantify this, we measured the longest streak of consecutive switch choices—instances where participants changed their assignment of items between characters during encoding. Since this was a yoked design, this measure was identical for both the Choice and Fixed groups. Linear mixed-effects models revealed no significant relationships between switch choices and recall performance ($\beta = -0.001$, $p = 0.847$, 95% CI [-0.01, 0.01]) and temporal clustering ($\beta = -0.0004$, $p = 0.960$, 95% CI [-0.02, 0.01]), and showed a marginal trend towards predicting stay transitions during recall ($\beta = 0.02$, $p = 0.083$, 95% CI [-0.003, 0.04]), suggesting that more switches during encoding may be associated with greater organization of memories around decision contexts.

Discussion

The present study shows that recall structure was shaped by whether an individual had agency over how items were assigned at encoding. Participants who had no agency over their choices relied more on temporal information to organize recall, where they were more likely to retrieve items in the order they were studied. In contrast, those who actively made choices were less dependent on temporal structure and instead organized their recall around their choices. This suggests that making choices during encoding creates a meaningful context that later guides memory organization.

While previous research demonstrated that agency enhances memory for chosen items (Ruiz et al., 2023a) and even extends to memory for choice-irrelevant content (DuBrow et al., 2019; Murty et al., 2015, 2019), our findings contrast with this work, as we found no overall memory benefit based on whether participants had agency over their choices. However, this aligns with recent work showing no differences in free recall memory between participants with and without agency using “choose-your-own-adventure” narratives (Li et al., 2024). In fact, one study from our lab even found that participants who actively explored an environment recalled less than those who explored passively (Houser et al., 2022). One possible explanation for these discrepancies is that the benefits of agency on memory may depend on the nature of the task. In free recall, agency may just shape how information is structured in memory without enhancing overall memory performance, though future work utilizing both recognition and free recall measures is needed.

Of central interest to the present study was the influence of agency on memory organization. While individuals typically recall information in a similar temporal order to which it was learned (Kahana, 1996; Sederberg et al., 2010), changes in encoding context have been shown to influence the degree of temporal clustering (DuBrow & Davachi, 2013, 2016; Rait et al., 2024). Although previous research manipulating motivational context did not find differences in temporal clustering across conditions (Horwath et al., 2023, 2024; Li et al., 2024), we found that participants who made choices during encoding exhibited less temporal clustering compared to those who had no control over their choices. This suggest that when individuals have agency over their choices, strictly relying on temporal information to organize memories may not be the most adaptive strategy.

Instead, individuals with agency structured their memories around relationships they formed through their choices. Previous work found that a shift in context leads individuals to group items with shared features together in memory (Heusser et al., 2018; Polyn et al., 2009b, 2009a). These findings also align with research from our lab on reward motivation, where reward creates a higher-order value category by which memories are adaptively organized (Horwath et al., 2023). Here, agency biased memory organization towards clustering based on the idiosyncratic choices individuals made. This is especially interesting given that participants were more likely to switch between characters during encoding. This suggests that the associations participants in the Choice group formed during encoding created a meaningful context for organizing their memories, one that superseded the temporal order of the items. In this way, recall was more influenced by choices than by temporal proximity, similar to how participants in previous work “jumped over” temporally closer items to recall items from the same category together (Chan et al., 2017). Notably, both groups experienced the same shifts in how items were assigned to each character, and across both groups, higher memory accuracy was associated with greater organization around decision context (see Table S4.2 for model details). Yet, despite these shared features, participants in the Choice group exhibited stronger decision clustering than those in the Fixed group. We provide novel evidence that it was not the shifts in character assignment that drove the effect, but rather the internal experience of agency—the subjective sense of making choices—that altered how participants structured their recall.

The current work adds to a growing body of literature on how context switching influences memory. While much of previous work focused on externally driven context shifts to investigate how context shapes memory (DuBrow & Davachi, 2013, 2014, 2016; Godden & Baddeley, 1975; Pettijohn et al., 2016; Pettijohn & Radvansky, 2018), the role of internally generated shifts has received less attention (Wang et al., 2023). In some cases, internal context shifts occur in response to an external cue (Horwath et al., 2023; Polyn et al., 2009b), which subsequently influence how memories are organized. In other cases, changes in context could be completely self-generated and independent of external instruction. Prior research suggests that both externally and internally driven shifts in goal states can create event boundaries that impair temporal order memory across the boundary (Wang & Egner, 2022). However, the present findings demonstrate a critical distinction: when context shifts are tied to a participant’s own choices—not those forced by an experiment—they alter memory organization in a unique way.

In conclusion, our findings demonstrate that while agency did not enhance overall memory performance, it restructured how participants organized their memories. Compared to participants with no control over their choices, those with agency showed reduced temporal clustering, suggesting that recalling items in strict temporal order may not always be the most adaptive strategy. Instead, participants with agency were more likely to organize memories around the relationships they constructed through their choices. This pattern highlights a shift in memory organization strategies, where agency may encourage clustering by meaningful associations rather than by temporal proximity. However, future work should explore whether this shift in organization reflects a tradeoff between different clustering strategies. Overall, these results contribute to a growing literature examining how motivational context shapes memory structure.

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CHAPTER V

GENERAL DISCUSSION

Our experiences are remembered in the context in which they occurred, such as the specific location or time that they happened. However, our environment is constantly changing. Previous research has demonstrated that our internal context shifts gradually over time but also can change abruptly in response to changing task demands (DuBrow et al., 2017; Polyn et al., 2009a). How context change contributes to memory organization in free recall is still unclear. Previous literature established that changes in context restructure memory (DuBrow et al., 2016; Polyn et al., 2009b). In the current dissertation, I aimed to: 1) examine how specific features of context change shape recall performance and organization and 2) test whether memory organization relates to drifting context representations in the hippocampus.

Features of context change shape recall performance and organization

A key goal of this dissertation was to investigate how qualitative aspects of context change influence free recall. Both **Chapter II and Chapter III** demonstrated that the rate of context change significantly influenced later memory. In **Chapter II**, rapid switching impaired memory only for novel contexts and not when switching between familiar contexts. In fact, when switching between familiar contexts, memory was just as strong when the context was changing rapidly as when the context remained stable, a finding replicated in **Chapter III**. Together, these findings indicate that the rate of context change influences the amount of information that individuals recall from memory, but only when the contexts are novel. This research highlights a critical interaction between context familiarity and rate of change. Additionally, in **Chapter III**, rapid context switching led to worse temporal clustering compared to slower context switching. This suggests that the rate of context change plays a crucial role in restructuring how participants organize their memories. Taken together, these findings highlight that the rate of context change not only influences how much is remembered, but also how memories are structured over time, underscoring its central role in shaping memory.

An important avenue for future research is to investigate how hierarchical context changes influence memory organization. The work in **Chapters II** and **III** examined how different rates of context change influenced memory, but each rate was presented in isolation—participants only experienced one at a time. However, in the real-world, contexts shift at multiple timescales simultaneously. For example, at a conference, the broad context (e.g., the event itself) might remain stable over hours, while local contexts (e.g., individual talks or conversations) change more rapidly. Previous research suggests that people can track multiple levels of event structure in parallel (DuBrow, 2022; Zacks et al., 2007). Behavioral experiments using event segmentation tasks demonstrated that people can consistently identify both fine-grained and coarser-grained events (Baldassano et al., 2017; Newtson, 1973; Sargent et al., 2013; Zacks et al., 2001), with fine-grained events grouped into larger, coarser-grained events. If events are organized hierarchically, this should have consequences for memory retrieval (Kurby & Zacks, 2011; Lee et al., 2022; Shin & DuBrow, 2021; Zacks, 2020). One study found that temporal order memory is preserved across shifts in high level context but disrupted by changes in low level context (Wen & Egner, 2022). However, surprisingly little work has investigated how the hierarchical organization of events influences memory organization, particularly during free recall. How does free recall memory reflect these nested structures? Does memory organization prioritize local (fast-changing) or global (slow-changing) context, or do these levels interact to shape retrieval dynamics? Investigating how recall transitions are structured across multiple timescales could provide new insights into how people navigate complex, hierarchical experiences in memory.

Much of the previous literature, including the work in **Chapters II** and **III**, used externally driven context shifts—such as changes in the physical environment or stimulus category—to investigate how context shapes memory (DuBrow & Davachi, 2013, 2014, 2016; Godden & Baddeley, 1975; Pettijohn et al., 2016; Pettijohn & Radvansky, 2018). However, the influence of internal context changes, such as changes in a person's goal, motivational, or emotional state, on memory organization have received less attention in prior literature (DuBrow et al., 2017; Wang et al., 2023). While previous studies used external cues to trigger a change in internal state (Horwath et al., 2023; Polyn et al., 2009b; Sahakyan & Kelley, 2002), disentangling their independent effects remains challenging (DuBrow & Davachi, 2013, 2014, 2016; Sols et al., 2017). **Chapter IV** uniquely examined memory organization in participants who made entirely self-generated switch decisions. Specifically, I manipulated agency during decision-making by allowing half of the participants to make their own choices, while the other half followed choices predetermined by other participants. Results showed that having agency during learning differentially influenced how participants structured their memories, where agency served as a context to organize memory. This work provides new insights into how internally generated context changes, such as having agency, structure memories and dovetail with previous work (Horwath et al., 2023; Polyn et al., 2009b). These results underscore the importance of considering both internal and external context shifts when studying memory.

The order in which items are recalled from memory reflects how memories are structured, with items that share a common context more likely to be retrieved, or clustered, together (Polyn et al., 2009a). Computational models of memory search posit that clustering occurs along multiple dimensions, including temporal proximity and source (e.g., task) context (Howard & Kahana, 2002; Polyn et al., 2009a). While it is most common to recall items in the temporal order in which they occur, as neighboring items share a similar temporal context (Howard & Kahana, 2002; Kahana, 1996; Sederberg et al., 2010; Sederberg et al., 2008), this may not always be the most adaptive strategy. Findings from this dissertation suggest a tradeoff between temporal and source-based clustering depending on encoding conditions. In **Chapter IV**, the results showed that participants with agency exhibited worse temporal clustering but better clustering based on the relationships formed through their choices (source clustering), compared to those without agency. These findings build on prior work showing that changes in context can produce recall transitions that are driven less by temporal proximity and more by event similarity (Heusser et al., 2018; Horwath et al., 2023; Lohnas et al., 2023; Polyn et al., 2009a, 2009b). The work in this dissertation extends this by demonstrating that agency can independently drive a similar shift. One possible mechanism underlying this shift is the resetting of temporal context at event boundaries (Pu et al., 2022). These results suggest that while temporal clustering is a dominant retrieval strategy, certain conditions can shift reliance toward source-based organization**.** This raises important questions about when and why individuals prioritize one strategy over another.

Memory organization relates to context representations in the hippocampus

A second goal of this dissertation was to determine whether free recall organization relates to gradually drifting context representation in the hippocampus. **Chapter III** found that manipulating the rate of context change at encoding produced parallel changes in hippocampal autocorrelation and temporal clustering. A higher context switch rate produced a relative decrease in both temporal clustering and hippocampal autocorrelation, while a slower context switch rate produced a relative increase. Most importantly, hippocampal activity during learning was positively correlated with temporal clustering during free recall. Collectively, these findings establish a critical link between context representations in the hippocampus and temporal clustering in free recall. This suggests that switching contexts at a high rate disrupts internal representations in the hippocampus, which in turn reduces temporal clustering during recall.

The result in **Chapter III** that autocorrelation was sensitive to the rate at which the external scene contexts changed was specifically observed in subregions of the hippocampus. However, network-level communication between the hippocampus and ventromedial prefrontal cortex (vmPFC), a node in posterior medial network (PMN), was found to play a role in maintaining stability within events (DuBrow & Davachi, 2016; Ezzyat & Davachi, 2011). Although the results from **Chapter III** did not find an effect of context change in the prefrontal cortex, it is possible that this region's engagement depends on its communication with the hippocampus. For instance, there is some evidence that the hippocampus and higher-order areas in the PMN are particularly sensitive to event-like structure at longer timescales (many seconds to minutes; Hasson, Chen, & Honey, 2015). This would suggest that the involvement of these regions would decrease as event duration decreases (and boundary frequency increases). Consistent with this, one study found that scrambling the content of video clips into random sequences of short segments (~3 sec) disrupted connectivity between the hippocampus and PMN. However, repeated exposure to the scrambled increased connectivity between those regions, suggesting a role in learning the longer events (repeated sequences) over time (Aly, Chen, Turk-Browne, & Hasson, 2018). Interestingly, this line of work dovetails with findings from **Chapter II** where repeated scene contexts help to offset the cost of rapid event switching on subsequent recall. Future work is needed, however, to assess how contextual repetition during rapid event changes influences hippocampal connectivity with other regions.

Episodic memory has been described as “mental time travel” (Tulving, 2002), where recalling an event reinstates the temporal context in which it was encoded, influencing the retrieval of items encoded nearby in time (Howard & Kahana, 2002; Polyn et al., 2009a; Sederberg et al., 2008). In **Chapter III,** we found that higher hippocampal autocorrelation (slower context drift) was associated with higher temporal clustering, meaning that items encoded in similar temporal contexts were recalled together. This effect emerged from experimentally manipulating the rate of context change during encoding, suggesting that external context shifts shape internal context representations and influence memory organization. However, **Chapter III** did not directly examine whether these internal context representations were reinstated during memory search. Previous work demonstrated that recalling an item reinstates not only its encoding-related neural patterns but also those of temporally adjacent experiences, supporting the role of temporal context reinstatement in guiding memory search (Folkerts et al., 2018; Kragel et al., 2015, 2021; Manning et al., 2011; Yaffe et al., 2014; Yoo et al., 2021; Zou et al., 2025). However, a key open question is how the rate of context change during encoding influences the extent of temporal context reinstatement during memory search. Does the amount of context stability during encoding alter what gets reinstated? One study found that when participants judged the recency of two items from the same category, the category identity of intervening items was reinstated, but this effect was significantly stronger when there was no category switch between probed items (DuBrow & Davachi, 2014). This suggests that context stability may enhance reinstatement, but it remains unclear whether this effect extends to temporal context reinstatement during free recall. Investigating neural reinstatement under conditions of rapid vs. gradual context change would provide direct insight into how encoding-related context representations are recovered during memory search.

A final question for future research surrounds the idea that remembering the context in which an event occurred is complicated by the fact that many experiences occur in similar contexts, such as repeatedly parking your car in the same parking lot. This similarity of contextual information can lead to interference between memories. There is abundant evidence from studies of rodents and humans that the hippocampus plays an essential role not only in binding stimuli to the context in which they occurred, but in differentiating similar contexts to avoid interference (Dimsdale-Zucker et al., 2018; Kyle et al., 2015). Indeed, recent evidence indicates that when contextual information is highly similar, this can actively drive hippocampal representations apart—a phenomenon termed repulsion (Chanales et al., 2017; Favila et al., 2016; Wanjia et al., 2021). At present, it is not clear whether or how repulsion of context representations in the hippocampus might influence behavioral expressions of memory. In particular, the phenomenon of repulsion is difficult to reconcile with the complementary role of the hippocampus in organizing or 'clustering' memories that share similar contexts. Specifically, studies of free recall in humans (Chan et al., 2017; Horwath et al., 2023; Polyn et al., 2009b), as well as studies in this dissertation, have shown that memories that share similar contexts during encoding tend to be clustered together during free recall. This raises an important question of whether repulsion of similar context representations in the hippocampus fundamentally changes the way memories are organized during free recall.

Conclusion

This dissertation provided novel evidence for how context change shapes memory organization. Specifically, across three studies, the results consistently demonstrated that manipulating features of context influences the order in which items are recalled, suggesting a potential tradeoff between temporal and source clustering. Furthermore, this work established a direct relationship between hippocampal context representations and behavioral organization of memories in free recall, underscoring the hippocampus' role in tracking and utilizing contextual changes. These findings highlight the dynamic role of context in memory recall, suggesting that both gradual and abrupt context changes shape how memories are structured. It is imperative to have a more nuanced understanding of not only the costs, but the potential benefits of changing contexts, which this dissertation addresses. I expect that these findings will be influential not only to researchers in the field of learning and memory, but also to psychologists and neuroscientists in the fields of attention, education, and computational modeling. Together, this work advances our understanding of how contextual dynamics shape memory organization and hippocampal activity, demonstrating its critical role in memory processes.

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APPENDIX A

CHAPTER II SUPPLEMENTARY MATERIALS

Immediate Recall				
	Estimate	***Est. Error***	***z value***	***p***
Fixed effects:				
(Intercept)	-1.51	0.12	-14.25	<0.001
switch rate	0.11	0.08	1.44	0.15
switch type	-0.02	0.08	-0.24	0.81
contextual familiarity	0.27	0.13	2.02	**0.04**
list half	0.30	0.04	7.75	<0.001
list number	-0.02	0.01	-1.93	0.05
switch rate: switch type	-0.24	0.11	-2.16	**0.03**
switch rate: contextual familiarity	-0.35	0.11	-3.10	**<0.01**
switch type: contextual familiarity	0.09	0.11	0.83	0.40
switch rate: switch type: contextual familiarity	0.39	0.16	2.48	**0.01**
Random Effects:				
σ^2	3.29			
$\tau_{00\ \text{word}}$	0.08			
$\tau_{00\ \text{subject}}$	0.24			
ICC	0.09			
N_{subject}	84			
N_{word}	240			
Observations	15980			
Marginal R^2 / Conditional R^2	0.014/0.103			

Table S2.1. Multilevel logistic regression model examining the interaction between switch rate, switch type, and contextual familiarity on percent recall for immediate recall. This model controlled for list number and list half (whether the word appeared in the first 12 or last 12 items in the list) as fixed effects and subject and word identity as random effects.

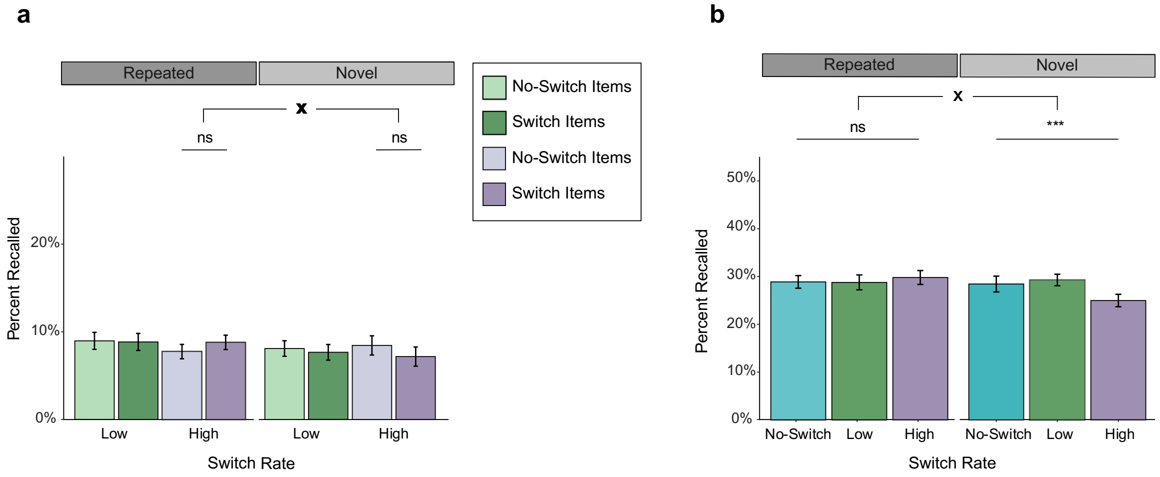

Figure S2.1. Final recall for experiments 1 and 2. a) Final Recall for Experiment 1. Overall, participants recalled 8.08% of total words during final recall, and there were no differences in the percent of words recalled between repeated (8.51%) and novel (7.67%) switches, $t(77.12) = 0.77$, $p = .44$, $d = .17$. There was no significant detriment to recall for rapidly switching to novel contexts, compared to not switching, $z = 1.54$, $p = .12$, partial $R^2 < .001$. Additionally, there was no statistically significant boost in performance during repeated switching for switch items in high-switch lists, $z = 1.13$, $p = .26$, partial $R^2 < .001$. However, and most importantly, similar to immediate memory, we observe a trend for the high list x contextual familiarity interaction, where recall for novel switches was slightly reduced compared to no-switch items than for repeated switches, $z = 1.87$, $p = .062$, partial $R^2 <.001$. **b)** Final Recall for Experiment 2. Participants recalled 28.34% of total words during final recall. There was no difference in the percent of words recalled between repeated (29.14%) and novel (27.55%) contexts, $t(161.48) = .73$, $p = .47$, $d = .11$. Results from final recall were largely similar to that of immediate recall for Experiment 2. Rapidly switching to novel, $z = -3.52$, $p = .0004$, partial $R^2 = .004$, but not repeated contexts reduced recall performance, and resulted in a reliable interaction, $z = 2.81$, $p = .005$, partial $R^2 = .003$. This pattern of results reflects those shown in Experiment 1 but are more robust. Error bars reflect within subject standard error for Experiment 1, and across subject standard error for Experiment 2. ns $p > .05$, *** $p <.001$.

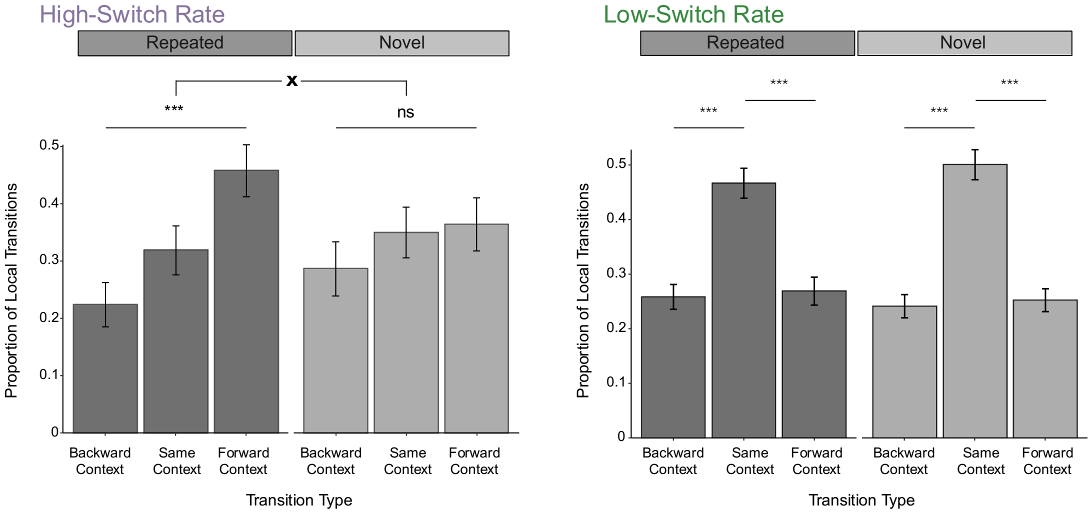

Figure S2.2. Proportion of local transitions by context for High and Low Switch rates for experiment 2. Here, we calculated the total number of transitions participants made to each type (backward, same, forward) and divided each context type by each participant's total number of recall transitions For the High Switch rate (left), results showed that when participants were switching back to repeated contexts, they made more forward than backward transitions, *t*(213) = -4.78, *p* <.001. In fact, there was a significant interaction, where more forward transitions were made, as compared to backwards, only in the repeated group, *t*(444) = -2.15, *p* = .032. This suggests that during rapid switching, participants tended to recall items from the following context only during repeated switching, despite being paired with a different external context. There were no significant differences between forwards and backwards transitions when switching to novel contexts, *t*(231) = -1.46, *p* = .144. In the Low Switch rate (right), participants transitioned significantly more to items in the same context compared to forwards or backwards in repeated, (Forwards: *t*(246) = -6.56, *p* < .001, Backwards: *t*(246) = -7.1, *p* < .001), and novel groups, (Forwards: *t*(249) = -9.87, *p* < .001, Backwards: *t*(249) = -9.98, *p* < .001). The Low Switch and high-switch results are unable to be directly compared due to differences in the number of items between each transition (2 vs. 4 items). Additionally, a comparison cannot be made to same context transitions for the high-switch rate, as there are more opportunities per list to transition to items in the following or previous contexts, as compared to the same context. Overall, the main comparison of interest is between repeated and novel contexts switches within switch rates. Error bars reflect across subject standard error. ns *p* > .05, ** *p* < .01, *** *p* <.001.

Supplementary Analysis 1

A Generalized Linear Mixed-Effect model was run to determine whether item position in the event predicted the percent of words that participants recalled, with subject, word identity, and response time as random effects and list number as a fixed effect. Items were labeled as boundary items if the previous item was from a different context. For the low-switch rate, preboundary items are items immediately preceding boundary items, and postboundary items are items immediately following boundary items. The third item in the list was not included in analysis. For the high-switch rate, since there are only two items, the items will be labeled as a boundary and non-boundary items. Primacy and recency items (first four and last four for low-switch, first two and last two for high-switch) were removed from this analysis.

Experiment 1

During immediate recall in the high-switch rate, there was no difference in percentage of words recalled between boundary and non-boundary items in the switch-back, z = 0.31, *p* =.76 or switch-novel, z = 0.23, *p* = .82, groups. Similarly, in the low-switch rate, there was no recall benefit for boundary items over preboundary, z = 0.08, *p* = .94 or postboundary items, z = -1.32, *p* = .19 when switching to repeated contexts. Likewise, there was no recall benefit for boundary items over preboundary, z = -0.26, *p* = .80, or postboundary items, z = -0.36, *p* = .72 in lists with novel context switches. This would suggest that item position did not contribute to the differences in condition and group discussed previously.

We found a similar result during final recall. In the high-switch rate, there was no difference between boundary and non-boundary items in lists with repeated, z = 0.60, *p* =.55 or novel, z = 1.34, *p* = .18, context switches. Additionally, In the low-switch rate, there was no recall benefit for boundary items over preboundary, z = 1.12, *p* = .26 or postboundary items, z = 1.36, *p* = .17 when switching to repeated contexts. Similarly, there was no recall benefit for boundary items over preboundary, z = 0.23, *p* = .82, or postboundary items, z = 0.07, *p* = .95 in lists with novel context switches. Taken together, these results show that there is no difference based on position of items, and participants are similarly likely to recall items from boundary and non-boundary positions across all conditions.

Experiment 2

During immediate recall in the high-switch rate, there was no difference between boundary and non-boundary items in either repeated, *z* = 0.29, *p* = .77 novel, *z* = 1.04, *p* = .30 context switching lists. However, in the low-switch rate, more boundary item words were recalled when switching to repeated contexts as compared to preboundary items, *z* = 2.25, *p* = .02. Surprisingly, there was no recall benefit for boundary items in lists with novel context switches over preboundary, *z* = -.34, *p* = .73 or postboundary items, *z* = -.22, *p* = .83.

We replicate this pattern during final recall. In the high-switch condition, participants recalled more boundary than non-boundary items in lists with repeated context switches, *z* = 2.74, *p* = .006. However, there was no difference between boundary and non-boundary items in lists with novel context switches, *z* = 0.77, *p* = .44. However, in the low-switch rate, more boundary item words were recalled in lists with repeated context switches as compared to postboundary items, *z* = 2.9, *p* = .004. As with immediate recall, there was no recall benefit for boundary items when switching to novel contexts over preboundary, *z* = .66, *p* = .51 or postboundary items, *z* = .49, *p* = .63.

Together, we found and replicated that in the high-switch rate, there was no memory difference in boundary or non-boundary items. This is consistent with previous work that also did not observe a boost in free recall of boundary items, perhaps because boundaries may selectively increase associative binding between an item and its context (Heusser et al., 2018). However, we did find that when the context was switching more slowly, participants recalled more boundary items than neighboring items only in the switch-back group. It is possible that we see enhanced recall at event boundaries in the low-switch rate and not the high-switch rate because the boundary creates an event in a stable context, like an oddball. However, if the context becomes blended as in the high-switch rate, there is a lack of a clear boundary.

Supplementary Analysis 2

Remote vs. local transitions

In Experiment 2, we demonstrated that when participants switch to repeated, compared to novel, contexts, they have less of an overall reliance on temporal organization. Yet, when investigating local transitions, there was less of a difference in the likelihood of transitioning to the same vs. forward or backward contexts for repeated vs. novel context switches, demonstrating more temporal structure. To reconcile these two seemingly contradictory findings, we investigated the relative proportion of local vs. remote transitions made by participants when switching to repeated vs. novel contexts across switch rates. Of their total transitions made, participants switching to repeated contexts made more remote (53.04%) than local transitions, z = 2.25, p = .025, OR = 1.13. This is reversed when switching to novel contexts, where participants made less remote (46.68%) than local transitions, z = -2.34, p = .019, OR = .88. Thus, remote transitions are significantly more likely when switching to repeated than to novel contexts, z = 3.12, p = .001, OR = 1.28. Therefore, the fact that local transitions are a smaller proportion of all repeated context transitions can help explain why participants simultaneously rely less on temporal organization overall but have higher local temporal structure with repeated context switches.

Replicating Experiment 1, participants who switched to repeated vs. novel contexts relied less on temporal information. This may seem counterintuitive, as we also found that when participants switched to repeated, compared to novel, contexts, there was less of a difference in the probability that their next transition would be from the same or forward context, demonstrating more temporal structure. We reconciled this by investigating the types of transitions made, and found that participants who switched to repeated contexts made more remote transitions. Since the scenes are returned to again and again in repeated context switches, this may explain why participants are making more long-distance transitions. This supports the framework that when scenes are repeatedly encountered, their representations may “blend” together such that recall transitions are likely to span the entire list.

APPENDIX B

CHAPTER IV SUPPLEMENTARY MATERIALS

Temporal Clustering			
	Estimate	***CI***	***p-value***
Fixed effects:			
(Intercept)	0.48	0.41 – 0.54	<0.001
Group	0.04	0.01 – 0.07	**0.012**
Mean Recall	0.14	0.05 – 0.23	**0.002**
List Number	0.00	0.00 – 0.00	**0.030**
Random Effects:			
σ^2	0.04		
$\tau_{00\ \text{Yoked Pair}}$	0.00		
ICC	0.02		
$N_{\text{Yoked Pair}}$	34		
Observations	657		
Marginal R^2 / Conditional R^2	0.026/0.041		

Table S4.1. Mixed-effects linear regression model examining the effect of Group (Choice vs. Fixed) and average number of words recalled per list (Mean Recall) on temporal clustering. The model also includes list number as a fixed effect and accounts for shared variance within yoked subject pairs (e.g., Pair A = Subjects 1 & 2) using a random intercept for Yoked Pair.

Stay Transition Probability			
	Estimate	***CI***	***p-value***
Fixed effects:			
(Intercept)	0.11	0.01 – 0.20	0.026
Group	-0.05	-0.10 – 0.01	**0.024**
Mean Recall	-0.17	-0.30 – -0.04	**0.012**
List Number	0.00	-0.00 – 0.00	0.336
Random Effects:			
σ^2	0.08		
$\tau_{00\ \text{Yoked Pair}}$	0.00		
ICC	0.04		
$N_{\text{Yoked Pair}}$	34		
Observations	649		
Marginal R^2 / Conditional R^2	0.018/0.060		

Table S4.2. Mixed-effects linear regression model examining the effect of Group (Choice vs. Fixed) and average number of words recalled per list (Mean Recall) on the probability of making stay transitions. The model also includes list number as a fixed effect and accounts for shared variance within yoked subject pairs (e.g., Pair A = Subjects 1 & 2) using a random intercept for Yoked Pair.