



Recall as a Window into Hippocampally Defined Events

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Abstract

■ We experience the present as a continuous stream of information, but often experience the past in parcels of unique events or episodes. Decades of research have helped to articulate how we perform this event segmentation in the moment, as well as how events and their boundaries influence what we later remember. More recently, neuroscientific research has suggested that the hippocampus plays a role at critical moments during event formation alongside its established role in enabling subsequent recall. Here, we review and explore the relationship between event processing and recall with the perspective that it can be uniquely characterized by the contributions of the hippocampus

and its interactions with the rest of the brain. Specifically, we highlight a growing number of empirical studies suggesting that the hippocampus is important for processing events that have just ended, bridging the gap between the prior and current event, and influencing the contents and trajectories of recalled information. We also catalogue and summarize the multifaceted sets of findings concerning how recall is influenced by event structure. Lastly, we discuss several exciting directions for future research and how our understanding of events might be enriched by characterizing them in terms of the operations of different regions of the brain. ■

INTRODUCTION

“Human experience unfolds continuously, yet memories tend to be organized into discrete episodes.”

– Sarah DuBrow

The above quote captures one of the most intriguing aspects about episodic memory: Our experience in the world is continuous, but our reexperiencing of it through our memories is not. Our minds readily segment and organize the continuous stream of information we experience, producing a set of distinct memories that then constitute our recollection of the past. These distinct psychological units of time (*events*) are typically delimited by points of significant or unexpected change in our internal and external environments (*boundaries*) such as initiating a change of topic in a conversation or walking through a doorway into a new room (Radvansky, 2012). The imposition of event structure on continuous experience is a ubiquitous aspect of human memory. Event boundary judgments have been found to be reliable across individuals and within individuals across time, and events are thought to encompass experiences across a broad range of timescales (Kurby & Zacks, 2008; Zacks & Swallow, 2007). Event structure has an immediate impact on how we process our environment, but more lastingly, it also determines how and what we later remember (Wang, Adcock, & Egner, 2024; Baldwin & Kosie, 2021; Shin & DuBrow, 2021; Radvansky, 2012; Kurby & Zacks, 2008; Speer & Zacks, 2005). Notably, this structure has been found to have a wide-ranging impact on episodic memory (memory

for specific details or instances from the past) in terms of what we later recall when cued or how we freely recall a series of events (Table 1).

Our processing of events retrospectively is often through the act of recall. Freely or otherwise, recalling past events provides a window into the structure and contents of our natural memories. The link between event processing and recall has been well studied across a diverse range of behavioral studies for decades, with a growing number of studies additionally providing insight into the underlying neural mechanisms at play. Specifically, the hippocampus, through its interactions with the rest of the brain, is thought to be a key structure involved in both event processing and our ability to recall the past (Baldassano et al., 2017; DuBrow & Davachi, 2016; Ben-Yakov & Dudai, 2011). The hippocampus has long been thought to play a necessary role in the recall of episodic memory. 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 event processing (see Ross & Easton, 2022, for a review). Taken together, these lines of literature strongly suggest that the hippocampus plays a fundamental role in linking event structure to how and what we recall.

Here, we aim to review the literature concerning how the hippocampus processes and organizes events as they unfold, with a focus on the consequences for later recall memory. We aim to provide a concise summary of the

Table 1. Behavioral Recall Effects of Event Structure by Boundary Manipulation and Type of Memoranda

<i>Boundary Manipulation</i>	<i>Type of Memoranda</i>	<i>Recall Effect(s)</i>	<i>Study</i>
<i>Boundary point</i>			
Activity change in navigation	Verbal free recall of walk details	Boundaries > other events	Jeunehomme and D'Argembeau (2020)
Task and category change	Verbal serial recall for faces/objects	Nonserial "jumps" to boundary > preboundary items	DuBrow and Davachi (2016)
		Boundary = other items	DuBrow and Davachi (2013)
Background color change	Verbal free recall for words	Boundary = other items	Heusser et al. (2018)
Change in physical space, computer windows, and narratives	Written free recall for words	Boundary not consistently > nonboundary items	Pettijohn et al. (2016)
Activity changes and movie cues	Typed free recall for movie details	Cued boundary > noncued boundary recall; Boundary < event middle recall (unedited movies)	Gold et al. (2017)
<i>Recall performance</i>			
Activity changes and movie cuts	Written free recall for movie details	Cut at breakpoint > cut at nonbreakpoint for recall containing breakpoints	Schwan et al. (2000)
Activity changes and movie summaries	Written free recall for movie details	Recall for breakpoint-keeping summaries > non-breakpoint-keeping summaries	Schwan and Garsoffky (2004)
Activity changes and commercials	Written free recall for movie details	Commercial at breakpoint > Commercial at nonbreakpoint	Boltz (1992)
Activity change (video)	Written or typed free recall for movie details	Better segmentation ability = better recall memory	Sargent et al. (2013)
		Better segmentation ability = better recall memory	Flores et al. (2017)
Change in physical space, computer windows, and narratives	Written free recall for words	Shift > no-shift	Pettijohn et al. (2016)
Physical room change	Free recall for object	Shift < no-shift	Pettijohn and Radvansky (2018)
	Written free recall for words	Two rooms > one room	Smith et al. (1978)
		Four rooms > two rooms > one room	Smith (1982)
Scene context change	Verbal free recall for words	Rapid changes to novel context < no context switches	Rait et al. (2023)
		Rapid changes to repeated contexts = no context switches	
		Slow changes to novel contexts = no context switches	
Narrative change	Typed free recall for story details	Two-shift > one-shift > no shift recall	Pettijohn et al. (2016)

Table 1. (continued)

<i>Boundary Manipulation</i>	<i>Type of Memoranda</i>	<i>Recall Effect(s)</i>	<i>Study</i>
<i>Spontaneous clustering</i>			
Task change	Verbal free recall for words	Within event > across event recall transitions	Lohnas et al. (2023); Polyn et al. (2009b)
Background color change	Verbal free recall for words	Within event > across event recall transitions	Heusser et al. (2018)
<i>Memory access</i>			
Task and category change	Verbal serial recall for faces/objects	Within event > across event serial recall	DuBrow and Davachi (2016); DuBrow and Davachi (2013)
	Cued sequential memory for item category	Within event > across event cued recall	Sols et al. (2017)
Narrative time changes	Cued recall	Within event > across event cued recall	Ezzyat and Davachi (2011)

relevant findings, with an added focus on the work of Dr. Sarah DuBrow as part of this memorial issue. We further aim to highlight what fruitful directions of future research might be as well as the possible conceptual insights offered by considering event processing through the perspective of a single brain region.

HOW DOES THE HIPPOCAMPUS PLAY A ROLE IN EVENT PROCESSING?

What Is an Event? What Is a Boundary?

Although exact definitions vary substantially (Yates, Sherman, & Yousif, 2023), events can be generally described as periods of relative stability or predictability across a set of relevant psychological features over time. Event boundaries, in contrast, can be established by significant changes along one or more of those feature dimensions (DuBrow, 2024; Radvansky, 2012; Zacks, Speer, Swallow, Braver, & Reynolds, 2007). For example, as seen in Figure 1, imagine that you are watching your favorite television show involving dragons and court intrigue. In

this case, events might be neatly captured by the different scenes in the show, with changes in characters, settings, and/or situations demarcating separate events. This definition of events could also be extended to include “internal” features such as feeling sad when a beloved character encounters a tragic betrayal.

One aspect of this definition is that changes in features can be relative to their predicted value, not necessarily their value a moment before. Broadly speaking, such moments are referred to as prediction errors, which are thought to be a psychologically and neurally multifaceted phenomenon (Bein, Duncan, & Davachi, 2020; Hutchinson & Barrett, 2019; Niv & Schoenbaum, 2008; Schultz & Dickinson, 2000). Here, events can be thought of as periods of high predictability, whereas boundaries involve moments where the predictions fail to sufficiently explain what is occurring, creating a prediction error (Shin & DuBrow, 2021; Rouhani, Norman, Niv, & Bornstein, 2020; DuBrow, Rouhani, Niv, & Norman, 2017; Gershman, Radulescu, Norman, & Niv, 2014; Zacks, Kurby, Eisenberg, & Haroutunian, 2011; Reynolds, Zacks, & Braver, 2007). This definition is generally consistent with event

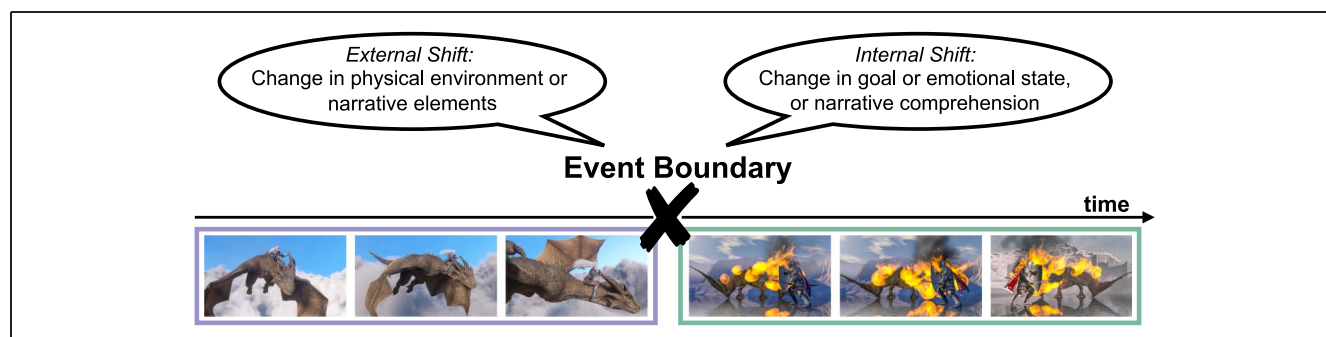


Figure 1. Schematic illustration of a narrative event separated by an event boundary. Experiencing a shift in the current environment, such as a scene cut denoted by different colors in frame outlines, can lead individuals to perceive an event boundary. Event boundaries can also be detected through more internal shifts, such as a change in mood when a tragedy befalls your favorite character (not depicted here).

segmentation theory, wherein individuals create internal mental models of the current event based on a combination of prior knowledge and perceptual input (Zacks et al., 2007). Per this theory, when there is an abrupt change in stimulus features, task, or goal states, the existing event model fails to predict the current situation, necessitating the establishment of a new model. This shift from one event model to another serves as an event boundary (Radvansky, 2012; Zacks et al., 2007). Thus, in the example involving your favorite television show, a scene cut serves as an effective event boundary not only because the contents on the screen change completely but also because the narrative that had been building up over the course of the scene is now completely unpredictable of what will come next.

However, prediction errors may not be completely necessary for generating event boundaries. Event boundaries can also occur when a relevant change is predictable or expected (Shin & DuBrow, 2021). For instance, the end of the episode of a television show you have seen multiple times can still be perceived as an event boundary even if you can come to predict when the episode will end. Empirical and theoretical work support this by showing that event segmentation occurs even with regularities in the environment (Schapiro, Rogers, Cordova, Turk-Browne, & Botvinick, 2013), when event changes are foreshadowed (Heusser, Poeppel, Ezzyat, & Davachi, 2016; Pettijohn & Radvansky, 2016), and when the inferred latent cause of ongoing experience changes (Shin & DuBrow, 2021). Recent research has also suggested that event boundaries can be generated independently of expectations (Siefke, Smith, & Sederberg, 2019) through changes in internal goal states (Wang et al., 2024; Wang & Egner, 2022). Although event segmentation theory proposes that event boundaries arise from surprise resulting from prediction errors, this suggests that boundaries can also manifest even in the absence of surprise, possibly through the reallocation of attentional resources (Yates et al., 2023; Baldwin & Kosie, 2021).

What Is a Hippocampally Defined Event?

The above definitions given for events and boundaries are couched in very general terms and could apply to a vast number of situations. The current review aims to constrain this conceptualization through focusing on the role of one key brain structure: the hippocampus. The hippocampus has long been thought to play a critical role in episodic memory (Eichenbaum, Sauvage, Fortin, Komorowski, & Lipton, 2012; Eichenbaum, Yonelinas, & Ranganath, 2007; Tulving & Markowitsch, 1998; Vargha-Khadem et al., 1997), but a series of findings in the past few decades has also suggested a role for the structure in event processing (Baldassano et al., 2017; DuBrow & Davachi, 2014, 2016; Ben-Yakov, Eshel, & Dudai, 2013; Ben-Yakov & Dudai, 2011). Below, we constrain our focus to this region in several complementary ways. First, we highlight

published work concerning event processing that report hippocampal involvement, either in terms of activity in the region or in terms of interactions with other regions of the brain. Second, when considering the sorts of features that matter the most in terms of characterizing these events, we can constrain them to be those that the hippocampus might be the most sensitive to. Specifically, we conceptualize these features as being largely synonymous with what memory researchers label “context,” as the hippocampus is thought to be vital for processing context-related information (Ranganath, 2010a, 2010b; Eichenbaum et al., 2007; Davachi, 2006). Context is an extremely broad and flexible term and intended here in an expansive sense, capturing both external (perceptual) and internal (mental) features, and also features that might shift suddenly (e.g., source context) and/or drift gradually (e.g., temporal context; DuBrow et al., 2017; Polyn, Norman, & Kahana, 2009a). Lastly, we narrow our primary focus to the subset of studies that consider how event processing is related to subsequent recall (whether cued, serial, or free), as recall is both a measure that is sensitive to event-like information in the world (e.g., time and order information), but also is thought to critically depend on the hippocampus (Staresina & Wimber, 2019; Smith & Milner, 1981; Scoville & Milner, 1957).

Hippocampal Interactions Supporting Within-event Representations

Event representations are typically stable, exhibiting insensitivity to moment-to-moment variations in sensory inputs (Zacks et al., 2007). This theorized stability has been bolstered by neuroimaging studies across modalities showing periods of stable patterns of brain activity punctuated by shifts at event boundaries (Silva, Baldassano, & Fuentemilla, 2019; Baldassano et al., 2017). Furthermore, fMRI research has suggested that in humans, regions in the posterior medial network (PMN) support the formation and contextually relevant application of event models (Ritchey & Cooper, 2020; Ritchey, Libby, & Ranganath, 2015; Ranganath & Ritchey, 2012). Although these event-relevant representations might rely upon PMN regions and not require the hippocampus per se (Zuo et al., 2020), there is evidence that the hippocampus communicates with these regions selectively during event processing.

In particular, network-level communication between the hippocampus and ventromedial prefrontal cortex (vmPFC; a node in PMN) might play a role in maintaining stability within events (DuBrow & Davachi, 2016). In an fMRI study, participants were presented with images of faces and objects one at a time and instructed to remember the order of the images while making a category-specific judgment. Event boundaries occurred when both the stimulus category and the category-specific task changed. The researchers found that greater functional connectivity between vmPFC and hippocampus was predictive of the degree to which participants integrated

within-event details in memory (DuBrow & Davachi, 2016). Another study using narrative stimuli revealed a gradual increase in activation in vmPFC as sentences progressed within an event, contrasting with reduced activation at event boundaries, suggesting an accumulation of event-relevant information (Ezzyat & Davachi, 2011). Taken together, along with the putative role of the vmPFC in integrating new information with prior associations (Schlichting & Preston, 2015), one possible interpretation is that hippocampal–vmPFC interactions promote the accumulation and integration of new information into the current, active event representation.

Events Are Hierarchical, Paralleling the Organization of the Hippocampus

Events are thought to be hierarchically organized, meaning that they can be identified at a range of temporal grains, from the smallest events that participants find natural and meaningful (fine-grained) grouped together into larger events (coarse-grained; Kurby & Zacks, 2008; Zacks & Swallow, 2007; Zacks, Tversky, & Iyer, 2001). For example, the act of watching your favorite television show is part of a larger, coarser-grained event of your overall time outside of work that evening. At the same time, within the event of watching the show, there are finer-grained, sub-events like following the plot, enjoying specific scenes, and reacting to on-screen developments. Neuroimaging studies have found that different brain regions support event segmentation at distinct timescales (Sava-Segal, Richards, Leung, & Finn, 2023; Antony et al., 2021; Baldassano et al., 2017). Using a naturalistic movie with events ranging from seconds to minutes, researchers employed a variant of Hidden Markov Modeling to characterize how different brain regions segmented events spanning multiple timescales (Baldassano et al., 2017). The researchers found that early sensory areas were sensitive to fine-grained changes, whereas higher-order areas, including regions in the PMN (angular gyrus and the posterior medial cortex) and hippocampus, were sensitive to longer-scale events. This was replicated in a study of individual differences, where researchers found that early sensory regions that are sensitive to fine-grained segmentations were most consistent across individuals, but higher-order, slower-segmenting regions showed more individual variability (Sava-Segal et al., 2023).

Although the exact nature of such hierarchical representations is being explored, there are some points of evidence suggesting a supporting role based on the functional organization of the hippocampus itself. That is, the hippocampal long-axis may represent a hierarchical gradient (Brunec et al., 2018), as the hippocampus differs in both structure and function along its long axis (dorsal–ventral in rodents and anterior–posterior in humans; Strange, Witter, Lein, & Moser, 2014; Poppenk, Evensmoen, Moscovitch, & Nadel, 2013; Moser & Moser, 1998). Research in rodents suggests a gradient representation of spatial scales, as

evidenced by increasing place field size from the dorsal to ventral hippocampus (Strange et al., 2014; Komorowski et al., 2013). Recent research in humans has begun investigating a similar gradient for episodic memory (Bouffard et al., 2023; Masís-Obando, Norman, & Baldassano, 2022; Collin, Milivojevic, & Doeller, 2021; Brunec et al., 2018). One study suggests that smaller scale events are represented in the posterior portion of the hippocampus, and larger scale events are represented in the anterior portion (Collin, Milivojevic, & Doeller, 2015). Although this line of work is nascent, it suggests one way in which hierarchical event structure might be directly supported in the hippocampus.

Hippocampal Involvement at Boundaries

In contrast to the stability and integration occurring within events, event boundaries are characterized by increased uncertainty and discontinuity because of the current event model becoming less predictable (Zacks et al., 2007). Numerous studies have observed an increase in hippocampal activity at event boundaries (Reagh & Ranganath, 2023; Reagh, Delarazan, Garber, & Ranganath, 2020; DuBrow & Davachi, 2016), and there are several accounts for this involvement (see Wang et al., 2024, and DuBrow, 2024, for related reviews).

First, it is possible that the hippocampus might play a role in encoding a “mnemonic” prediction error signal per se that is used by the brain to infer an event boundary. That is, in the course of processing an event, the hippocampus generates predictions of what will follow and compares that to incoming information. If the incoming information does not match the prediction, then the hippocampus produces a mismatch/prediction error signal (Chen, Cook, & Wagner, 2015; Kumaran & Maguire, 2006; Lisman & Grace, 2005; Hasselmo, Wyble, & Wallenstein, 1996). Accordingly, increased activity at event offsets would be related to the co-occurring boundary.

Second, there are processes facilitated by mnemonic prediction errors that influence how the brain samples new information in the environment. For example, recent research suggests that after a prediction error, hippocampal activation is associated with a shift in processing toward the encoding of novel information (Bein et al., 2020). Speculatively, at boundaries, individuals must sample information from the new event, requiring a reorienting of attention toward incoming information to retrieve appropriate knowledge and improve predictions (DuBrow, 2024; Pradhan & Kumar, 2022; Baldwin & Kosie, 2021; Zacks et al., 2007). There is some evidence that the hippocampus might play a role in goal-driven attention (Aly & Turk-Browne, 2016), suggesting a possible additional involvement related to attentional reorienting, although further, targeted work is necessary.

Lastly, event boundaries are also associated with increases in hippocampal activity that relate to subsequent memory for the preceding event (Barnett et al., 2022;

Michelmann et al., 2021; Baldassano et al., 2017; Ben-Yakov et al., 2013; Ben-Yakov & Dudai, 2011), suggestive of a retrospective role for the region. We review some evidence for these retrospective processes in a later section.

HOW MIGHT THE HIPPOCAMPUS SHAPE SUBSEQUENT RECALL OF EVENTS?

Memory Is Shaped by Event-like Context

In humans, the creation of memory's structure is thought to be supported by representations of context. Most notable in terms of understanding the relationship between context and event processing are two classes of context in particular: temporal context and source context (Polyn et al., 2009a). Temporal context is thought to be a slowly drifting representation of context that effectively "tags" memories with a time-dependent contextual marker (Polyn et al., 2009a; Howard & Kahana, 2002). Accordingly, even in trial-based experiments where individual items might not be predictable, when two temporally adjacent items are associated in memory with the same slowly drifting context representation, it establishes an indirect pathway through which they might become linked over time (DuBrow et al., 2017). Source context reflects the content of the information present at encoding beyond this drifting temporal representation. This can include features such as the type of stimulus used or the task

that participants are instructed to perform (DuBrow & Davachi, 2013; Polyn, Norman, & Kahana, 2009b; see Figure 2A). These contextual factors have been established in studies of free recall, which show that recall transitions (successive items recalled) are made to items studied in similar contextual states—temporal or source (Lohnas, 2024; Lohnas, Polyn, & Kahana, 2015; Polyn et al., 2009a; Polyn & Kahana, 2008; Sederberg, Howard, & Kahana, 2008; Kahana, 1996). For example, free recall in the absence of significant source context changes (e.g., event boundaries) is often in temporal order (near the start or end of a list of words; Kahana, Diamond, & Aka, 2022; Polyn & Cutler, 2017; Polyn et al., 2009a; Sederberg et al., 2008; Howard & Kahana, 2002; see Figure 2B). In our conceptualization focusing on the perspective of the hippocampus, these contextual states can be thought of as synonymous with events, with periods of contextual stability (or slight drift) existing within events, and boundaries marked by sharper shifts in context (such as those present across changes in source context; DuBrow et al., 2017).

How Is Recall Shaped by Within-event Structure?

Free recall provides unique insight into the representation of information within events. Although free recall is definitionally unconstrained and participants can recall items in any order, there is a wealth of data to suggest that when there is a salient change in the environment, memory

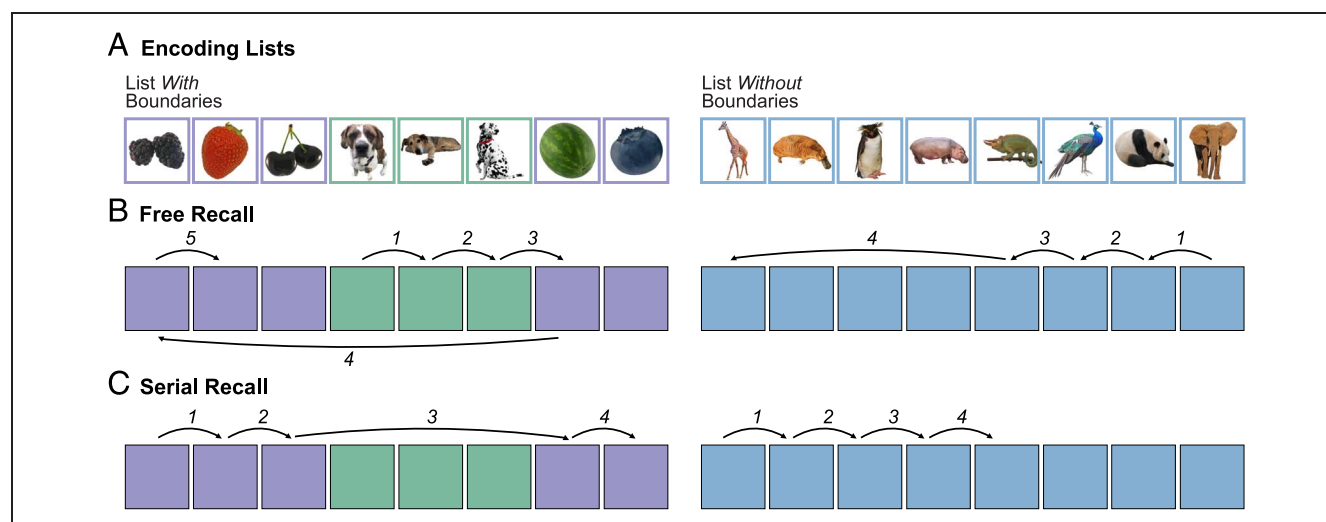


Figure 2. How event structure influences recall transitions. (A) Encoding list with event boundaries (left) and encoding list without event boundaries (right). Each color frame represents a unique task-related context (visual category of stimulus). (B) How event structure influences free recall organization. Colored squares represent items from encoding with color corresponding to encoding task context. Arrows represent a representative example of recall transitions (the sequence that items were recalled in). Overall, the presence of event boundaries in a list (left) enhances recall performance and can often increase memory for boundary information while facilitating task-related, context-based memory organization (see text for details). The first recall is depicted here as starting in the middle of the list, instead of at the beginning or end of the list (Murdock, 1962), as previous literature suggests that boundary items tend to be recalled first in a recall sequence (Polyn et al., 2009b). On the other hand, in lists without boundaries (right), there is a stronger tendency to recall end-of-list items first while recalling items together that occurred closer together in time (Howard & Kahana, 2002). (C) How event structure influences serial recall transitions. Colored squares represent items from encoding with color corresponding to encoding task context. When participants are instructed to recall items in the order they were presented, the presence of an event boundary in a list leads to more serial transitions within an event rather than across an event boundary (arrows; left). However, although the recall order is constrained, transitions tend to also be made nonserially to boundary items (e.g., Transition 3; DuBrow & Davachi, 2013, 2016). These dynamics are not present when there are not list boundaries (right).

tends to be structured, such that items presented in the same event tend to be remembered, or “clustered” together (Polyn, Kragel, Morton, McCluey, & Cohen, 2012; Polyn et al., 2009a, 2009b; Smith, 1982; Hintzman, Block, & Inskip, 1972; Murdock & Walker, 1969; Figure 2B). For instance, in one study, when the task context switched halfway through a studied list, relatively more recall transitions were made to items studied with the same task rather than transitioning across task-shift boundaries (Polyn et al., 2009a, 2009b). Another study found that participants “leaped over” over temporally closer items to recall items that had been studied in a similar task context (Chan, Applegate, Morton, Polyn, & Norman, 2017). Relatedly, research showed that recall transitions were more likely to occur from boundary items to nearby within-event items than from preboundary items to items across an event boundary (Lohnas, Healey, & Davachi, 2023; Heusser, Ezzyat, Shiff, & Davachi, 2018).

This dynamic generally holds outside of free recall tasks, whereby recall is either cued by the experimenter or participants are instructed to recall items serially. For example, in a set of behavioral findings, participants made more accurate serial recall transitions to items that appeared within the same event rather than to items that appeared across an event boundary (DuBrow & Davachi, 2013, 2016; Figure 2C). Similarly, cued sequential recall (remember stimulus that followed the cue at encoding) performance has been found to be worse when cues require participants to recall information spanning an event boundary, compared with when they require participants to recall an item from the same event (Sols, DuBrow, Davachi, & Fuentesmilla, 2017; Ezzyat & Davachi, 2011). These studies suggest that items that appear in the same event are more likely to be “bound” together, facilitating clustering of those memories. This associative binding seems to be reduced when items span an event boundary, regardless of recall strategy.

Influence of Boundaries on Overall Recall Memory

Research using both the segmentation of continuous events (Schwan, Garsoffky, & Hesse, 2000; Flores, Bailey, Eisenberg, & Zacks, 2017) and the insertion of event boundaries through shifts in experimental context (Pettijohn, Thompson, Tamplin, Krawietz, & Radvansky, 2016; Smith, Glenberg, & Bjork, 1978) have demonstrated that that free recall performance is higher when the experience contained an event boundary. In fact, this is particularly the case when an event boundary is reinforced, for example, by the addition of a film cut or commercial at the point of a predetermined boundary (Schwan & Garsoffky, 2004; Schwan et al., 2000; Boltz, 1992). Moreover, it is possible that not just the quantity but the quality of boundaries might help subsequent recall. That is, as noted above, participants often agree on the location of event boundaries, for example, in movies (Zacks & Swallow, 2007). Participants with better segmentation judgments (i.e., better

agreement with the group; Flores et al., 2017; Sargent et al., 2013) and more similar neural event boundaries (Sava-Segal et al., 2023) tended to have better subsequent recall performance, suggesting that it is not just the number or presence of boundaries per se that matters.

Boundary enhancement of subsequent recall is also associated with increased hippocampal activation patterns at the end of events during encoding (Reagh & Ranganath, 2023; Barnett et al., 2022; Michelmann et al., 2021; Reagh et al., 2020; Baldassano et al., 2017; DuBrow & Davachi, 2016; Ben-Yakov et al., 2013; Ben-Yakov & Dudai, 2011). Research suggests that hippocampal involvement at event boundaries may reflect rapid memory reactivation, or possibly replay, of the preceding event to promote continuity across episodes (DuBrow, 2024; Bilkey & Jensen, 2021; Clewett, DuBrow, & Davachi, 2019). Scalp EEG data in humans have provided support for the view that boundaries can serve as brief breakpoints during which reactivation can occur (Silva et al., 2019; Sols et al., 2017). In one EEG study, context shifts triggered the activity patterns from the just-encoded event to be reactivated rapidly after event offset (~200 to ~800 msec). The extent of the reactivation at boundaries was associated with participants’ later recall memory (Sols et al., 2017). These researchers suggest that this memory reactivation at event boundaries can represent a way to integrate different events that share contextual information. Therefore, although event boundaries separate events, the coactivation of the preceding and current events can help promote temporal memory organization across boundaries (Silva et al., 2019).

Similar responses have also been observed using fMRI. In one line of work, researchers presented participants with brief movie clips and examined hippocampal activity immediately following each clip. They found that hippocampal activity was time-locked to the offset of the clip, which correlated with later memory (Ben-Yakov & Dudai, 2011; Figure 3A). This hippocampal offset response occurred for isolated clips, as well as clips that were immediately followed by unrelated clips (Ben-Yakov et al., 2013). This suggests that event offsets, rather than the beginning of a rest period, are more likely to trigger hippocampal activity. Similarly, during continuous movie viewing, researchers found that the end of an event as represented by regions in PMN (angular gyrus and posterior medial cortex) potentially triggered the hippocampus to encode information about the preceding event into episodic memory. This was demonstrated by showing that the hippocampal response at the end of events correlated with the degree of cortical reinstatement during recall, particularly related to how long participants spent recalling the preceding event (Baldassano et al., 2017). Another fMRI study suggested that increased connectivity between the hippocampus and regions in the PMN is associated with greater subsequent recall of the event preceding the offset (Barnett et al., 2022). Interestingly, one study found that the effect of hippocampal activation on memory for the preceding event depended on whether the end

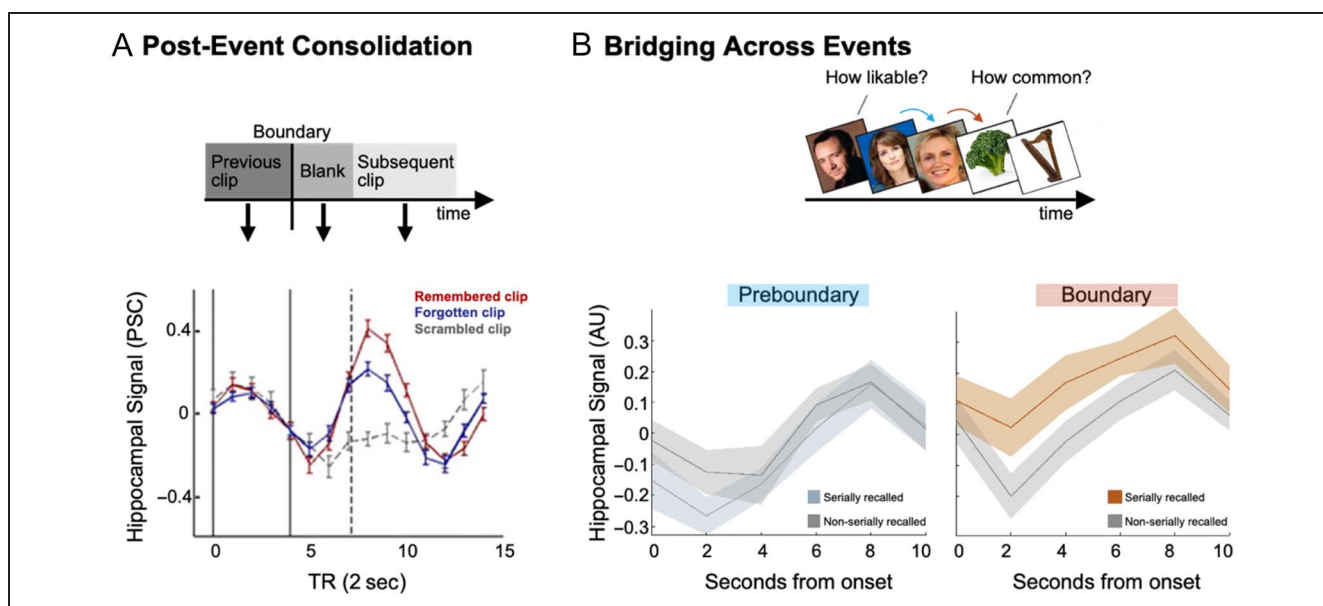


Figure 3. The role of the hippocampus at event boundaries. (A) Researchers presented participants with brief narrative movie clips (narrative and visually scrambled; top) and examined hippocampal activity during blank periods immediately following each clip (bottom). They found that right hippocampal activity (PSC: percent signal change, z scored) was time-locked to the offset of the clip, which was higher when the clip was subsequently remembered versus forgotten (adapted with permission from Ben-Yakov & Dudai, 2011). (B) In a task context-switching study, participants were presented with images of faces and objects one at a time and instructed to remember the order of the images while making a category-specific judgment (top). Event boundaries occurred when both the stimulus category and the category-specific task changed. fMRI analyses (bottom) revealed greater activity (AU = arbitrary units) in the mid-hippocampus for boundary items that were subsequently serially recalled (vs. recalled nonserially), but not for preboundary items (vs. recalled nonserially; adapted with permission from DuBrow & Davachi, 2016).

of the event was expected or surprising. Specifically, they found that greater hippocampal activation following an expected ending was associated with the preservation of memories, but led to memory updating following a mnemonic prediction error (Sinclair, Manalili, Brunec, Adcock, & Barense, 2021). Taken together, these findings suggest that the hippocampus, possibly through interactions with PM cortical regions, might support event encoding through reactivation or retrospective integration at event boundaries.

Memory for Boundary-based Information

As discussed above, the mere presence of event boundaries might facilitate subsequent memory. However, what about memory for the boundary information itself? Although several free recall studies have demonstrated a memory advantage for boundary items, others have failed to establish a consistent benefit for recalling such items. 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 task shift (Polyn et al., 2009b; Figure 2A). A similar boundary enhancement was observed using naturalistic navigation (Jeunehomme & D'Argembeau, 2020). In addition, in a study of sequential recall containing event boundaries, although the recall order was constrained, participants still tended to make more nonserial “jumps” to boundary information during recall (DuBrow &

Davachi, 2016; Figure 2B). 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 et al., 2007). However, one serial recall study with event boundaries characterized by changes in both image category and category-specific task found no difference in overall recall performance between boundary and nonboundary items (DuBrow & Davachi, 2013). Similar results were observed with perceptual changes (Heusser et al., 2018), changes in physical location, changes in computer windows, or situational changes in a narrative (Pettijohn et al., 2016), where there was no consistent boost in free recall for boundary items. 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, Zacks, & Flores, 2017). Determining the specific conditions under which recall memory for boundary information is enhanced is an important avenue for future research.

There are a few lines of work suggesting that the impact of boundary effects on memory is related to hippocampal and prefrontal cortical involvement. One such study found that at the moment the event boundary occurred,

activation in mid-hippocampus and left ventrolateral prefrontal cortex (vlPFC) were both related to whether boundary items would be correctly serially recalled (DuBrow & Davachi, 2016; Figure 3B). A similar effect was observed using cued recall of sentences in a narrative, where participants' boundary memory was correlated with activity in regions including left vlPFC (Ezzyat & Davachi, 2011). Although event boundaries are typically associated with discontinuity, such that boundaries impair memory for the temporal order of items (DuBrow & Davachi, 2014), the hippocampus and vlPFC may maintain continuity across change points. This function serves to bridge temporally adjacent events and complements the role of hippocampal interactions with vmPFC to promote integration within events. This would allow for the preservation of some temporal structure via integration, leading to success in recalling items that span a boundary (DuBrow, 2024; Clewett et al., 2019; Davachi & DuBrow, 2015).

CONCLUDING REMARKS AND FUTURE DIRECTIONS

Taken together, the above findings provide an overview of how the hippocampus plays an important role in creating and recalling event structure. Specifically, the hippocampus supports within-event cohesion and event-level organization through interactions with cortical regions and also is sensitive to event boundaries in a number of ways. Importantly, the hippocampus also is thought to perform operations at event encoding that shape the trajectories of subsequent serial and free recall. In addition to these fundamental aspects of how we mentally segment, organize, and remember our continuous experience, there are a number of promising directions of ongoing research that will likely add to what is known about how the hippocampus influences event processing.

Can Too Many Boundaries Be Disruptive to Memory?

In the real world, different situations are often accompanied by dramatically different numbers of events and boundaries. For instance, a postal worker can spend their whole day delivering packages to different houses or only a few large apartment building mailrooms. How might this influence their memory? Research suggests that the benefits of an event boundary on memory performance may be magnified with increasing numbers of event boundaries (Jafarpour, Buffalo, Knight, & Collins, 2022; Smith, 1982, 1984). In narratives with event shifts, stories with two shifts enhanced overall recall performance compared with those with only one shift (Pettijohn et al., 2016), although there was no concurrent memory improvement for information at the event boundary. Taken together, the above findings are suggestive that more boundaries might always result in better memory.

However, one recent study from our group found that memory for boundary information changed depending on the frequency of the boundaries and, indeed, too many boundaries might relatively impair recall. Specifically, the frequency of event boundaries was manipulated by switching background scenes at different trial intervals during the encoding of a list of words (either every two or every four trials). Participants showed enhanced free recall for words paired with boundary, as compared with non-boundary, scenes when switching back and forth between two scenes slowly (fewer event boundaries) but not when switching rapidly (more event boundaries; Rait, Murty, & DuBrow, 2023). It is possible that enhanced recall for information at event boundaries is observed with slower, rather than rapid, switching because the boundary in the slower case creates a salient event in a stable context, akin to an oddball effect (Ranganath & Rainer, 2003). However, when switching between two scene contexts rapidly, the internal context representation may become more of a blend of information related to each of the two contexts (Rait et al., 2023; Polyn et al., 2009a, 2012), leading to less salient event boundaries and worse memory.

The influence of multiple event boundaries on memory performance may further vary depending on the specific characteristics of the presented events. For example, if asked to recall the types of packages delivered, the postal worker's memory may differ depending on if it was their first day or if they were very familiar with the route. This was demonstrated in a context switching paradigm used by our group, where we manipulated the frequency of switches and prior experience with scene contexts participants were switching between (repeated vs. novel). We found that rapid switches to multiple novel scene contexts (more event boundaries) led to worse free recall performance, whereas rapid switches between repeated scene contexts or slower switches to novel scene contexts (fewer event boundaries) did not hinder overall free recall performance (Rait et al., 2023). Future research is needed to further examine how the qualitative features of events (e.g., relative novelty, level of similarity) interact with boundary frequency.

The aforementioned studies highlight the importance of the quantity or frequency of event boundaries in terms of broad impacts on memory, although they do not necessarily speak to one factor or the other. So, questions remain in terms of how the quantity versus frequency of event boundaries influences memory. Furthermore, it also remains to be seen what the role of the hippocampus is in such situations. 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, when the same scrambled movies were repeatedly presented, they found increased connectivity between those regions with repetition, 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 the above findings wherein repeated scene contexts help to offset the cost of rapid event switching on subsequent recall (Rait et al., 2023). Future work is needed, however, to assess how contextual repetition during rapid event changes may engage the hippocampus.

How Does the Brain Handle Multiple Active Event Streams at Once?

Humans are generally proficient at performing multiple tasks at the same time, raising the possibility that multiple event structures or “streams” can be maintained in parallel. For instance, pilots successfully fly planes while attending to their navigation, receiving instructions from air traffic control, and keeping track of the weather. The boundaries across these streams do not even need to be aligned (the pilot could successfully land the plane while continuing a conversation with the co-pilot). Theoretically, then, it might be possible that event model updating is done incrementally rather than holistically or perhaps the hierarchical nature of event representation can be flexibly extended to parallel streams of events, which might have similar temporal grains (DuBrow, 2024; Shin & DuBrow, 2021; Zacks et al., 2007). Would such processes be supported by the hippocampus? As discussed above, there is a tentative link in terms of the hierarchical gradient within the long axis of the hippocampus (Brunec et al., 2018; Poppenk et al., 2013); however, this line of inquiry largely awaits future research.

Interestingly, this line of research might inform other domains that have not been strongly tied to hippocampal involvement. For example, individuals vary in how much they engage in multitasking, which has important behavioral consequences for performance (Wammes et al., 2019; Uncapher & Wagner, 2018). Previous research has explored the relationship between multitasking and various cognitive domains for chronically heavy versus light multitaskers (Ophir, Nass, & Wagner, 2009). An open question remains as to how event structure influences our ability to multitask and the consequences for memory. Future research employing multitasking designs holds promise not only for uncovering individual variations in memory performance but also for evaluating the question of whether hippocampal representations are task specific or serve broader, domain general purposes (Han et al., 2023).

Using the Brain to Define Event Types

Although the above future directions each suggest potentially rewarding directions for empirical research, the

emphasis of the current review on the hippocampus and event processing also highlights a perspective with which to conceptualize event processing more broadly. That is, there is a rich literature establishing how psychological features shape our ongoing processing of event structure in the world (Shin & DuBrow, 2021; Zacks, 2020; Clewett et al., 2019; DuBrow et al., 2017; Zacks et al., 2001, 2007). A complementary perspective might seek to understand how events can be defined based upon which region(s) of the brain support their creation and/or are sensitive to their boundaries. This perspective would suppose the existence of hippocampally defined events, as reviewed above, and offers to enrich our understanding of event processing in several ways. First, by assessing the degree of hippocampal involvement across various experimental factors thought to facilitate event formation, one might produce a useful way to further taxonomize the myriad psychological variables thought to be involved. That is, there ultimately might not be a singular definition of an event in psychology per se (Yates et al., 2023), but rather different subtypes definable based on the conjunction of their psychological and neural features. Second, better characterizing how the hippocampus enables event processing would allow better bridging of psychological and neural theory. For example, although events are often couched in terms of fundamental factors such as space and time, it remains relatively under-explored how psychological event structure might relate to representations of those factors supported by the hippocampus (and vice versa; Eichenbaum, 2017). Lastly, a core assumption of the current review is that the hippocampally defined events provide a complementary understanding to how we temporally segment incoming information. That is, such events provide further insight into how we organize and remember that information once that moment has passed.

More speculatively, this perspective could conceivably be extended to other structures in the brain. For example, an important characteristic of event boundaries is the lack of predictability of the current situation considering the immediate past. Although the hippocampus is one structure that is sensitive to mismatches between predictions and reality and other discontinuities (Maurer & Nadel, 2021; Lisman & Grace, 2005), other structures have similar properties in domains beyond episodic memory. It is possible, then, that these other structures might be sensitive to event properties like the hippocampus, although the relevant features and nature of the predictions might vary. This could include structures like the basal ganglia, which produces prediction errors in response to unlikely events (Wyrobnik, van der Meer, & Klostermann, 2023; Zacks, 2020), but also, potentially, speculatively could be extended to cortical structures sensitive to various grains of perceptual or temporal information (Hutchinson & Barrett, 2019; Hasson et al., 2015; Rao & Ballard, 1999).

How we make sense of our ongoing and past experiences relies on how we segment and organize them. Here,

we have highlighted the multifaceted way in which the hippocampus might enable these fundamental processes. Indeed, a focus on event segmentation and recall provides a unique perspective with which to highlight the numerous hippocampal mechanisms critical for both refining our internal models of the world, but also optimizing subsequent memory of episodic details.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were $M(\text{an})/M = .407$, $W(\text{oman})/M = .32$, $M/W = .115$, and $W/W = .159$, the comparable proportions for the articles that these authorship teams cited were $M/M = .549$, $W/M = .257$, $M/W = .109$, and $W/W = .085$ (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this paper report its proportions of citations by gender category to be: $M/M = .435$; $W/M = .231$; $M/W = .204$; $W/W = .13$.

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