

Events and Boundaries

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<i>Please provide a concise abstract for the chapter (100–250 words).</i>	
<p>Human experience unfolds continuously, yet memories tend to be organized into discrete episodes. Event Segmentation Theory provides a framework for understanding this discretization by suggesting that ongoing experience is characterized by extended periods of high predictability (events) punctuated by transitions between stable states (event boundaries). The chapter begins with a brief introduction to theories of event segmentation in perception and language. Then, the majority of the chapter reviews interactions between event processing and episodic memory, drawing from theoretical, behavioral and neuroscience literatures. The first section of this review focuses on boundary-related memory processes, including transient memory enhancements, boundary-triggered reinstatement or replay, and the discretization of neighboring events in memory. The second section focuses on processing that unfolds within events, including working memory maintenance, retrieval of schematic information, and ongoing prediction. Together, these data highlight a fundamental relationship between online event segmentation and episodic memory. Finally, some key challenges and open questions for future research are discussed.</p>	
<i>Please suggest 5–10 keywords that can be used for describing the content of the chapter.</i>	
<p>Event segmentation, boundaries, situation models, temporal context, replay, prediction, working memory, schemas, episodic memory, hippocampus</p>	

1) Event Segmentation Theory

As we experience the world, we make predictions about what will occur next based on our current situation. From moment to moment, we tend to expect relatively small changes. These predictions may derive from an internal *event model* -- a set of expectations for an ongoing experience derived from a combination of prior knowledge and details about the current situation (Zacks et al., 2007). For example, there are certain expectations one might have about ordering food at a restaurant – it involves being at a table, looking at a menu, interacting with waitstaff, and introspecting about what one would like to eat (see Figure 1). This schematic information may be active in mind during any “ordering food” event. An event model integrates this information with details regarding the current situation (e.g., the specific restaurant, menu items, etc.) to generate predictions for the ongoing experience. Importantly, when the event model’s predictions are no longer accurate, the model is updated. The time point at which the updating occurs is called an *event boundary*. In the “ordering food” example, the menu being taken away violates the predictions of the current event model. Thus, it may serve as an event boundary, signaling that the previous event has ended and a new event should begin.

----- Insert Figure 1 -----

The framework just described was put forth by Event Segmentation Theory (EST; Kurby & Zacks, 2008; Zacks et al., 2007) to explain how continuous activity is segmented into meaningful subunits to guide attention and memory. The notion of an event as a discrete unit was originally inspired by work in perception, specifically the problem of object recognition (Zacks & Tversky, 2001). Parsing the visual landscape into objects shares many of the same challenges as parsing ongoing activity into events. Both processes involve the discretization of continuous dimensions along spatial or temporal boundaries, respectively, and can operate at different levels of abstraction – groups of spatial elements for objects or timescales for events. Importantly, just as object recognition is critical for understanding complex visual landscapes, event segmentation can be beneficial for facilitating ongoing perceptual processing.

In addition to visual perception, EST has been heavily influenced by work in language comprehension. Researchers theorize that as individuals process narratives, they construct mental models, called situation models, that track the connections between narrative elements (Bower & Morrow, 1990). According to the Event Indexing Model, there are five key features that are constantly monitored -- space, time, goals, actions, and characters -- such that a change in any one of them triggers updating of the corresponding index of the situation model (Zwaan, Langston, et al., 1995). Thus, situation models, like event models, represent unique instances of more general situational categories or “event schemas” (Zacks et al., 2007; Zwaan & Radvansky, 1998). This allows prior schematic knowledge to inform the current situation while also incorporating idiosyncratic features of the current environment. One key difference between the theories is how updating is triggered. In the Event Indexing Model, updating occurs whenever at least one feature changes, while in EST, updating occurs when the predictions of the event model are violated. This is an important theoretical distinction, as the latter allows for some amount of low-level feature change to occur without the need for updating (i.e., change predicted by the current event model; for discussion, see Richmond & Zacks, 2017; Shin & DuBrow, 2020).

As introduced here, theories from perception and language comprehension have led to the development of a broad framework of event segmentation, which has implications for many aspects of cognition. This chapter focuses on the role of event segmentation in episodic memory. There is now substantial evidence that segmentation and memory processes are closely related. For example, a common method for measuring segmentation is to simply ask individuals to identify boundaries between meaningful units of activity while reading text or watching a movie (e.g., Newtonson & Engquist, 1976; Zacks et al., 2009). Using this approach, researchers have shown that the ability to detect event boundaries, as measured by the degree of correspondence with normative segmentation, correlates across individuals with episodic memory performance for the segmented events (Kurby & Zacks, 2011; Zacks et al., 2006), even when controlling for other cognitive abilities (Sargent et al., 2013). Moreover, during encoding, instructing participants to perform a segmentation task improves long-term memory retention relative to instructing participants to remember content for a later memory test (Flores et al., 2017). These data suggest that spontaneous segmentation of experience, as proposed by EST, may be adaptive not only for ongoing processing but also for the long-term memory of those experiences (Clewett et al., 2019; Radvansky & Zacks, 2017).

This chapter will review event segmentation processes that have been theorized to influence memory, organized according to whether they occur at the boundaries between events or during the events themselves. First, at the moment a boundary occurs, attention may be reallocated to the external environment in order to sample information relevant for updating the event model (Baldwin & Kosie, 2020; Zacks et al., 2007). This attentional shift may enhance encoding of concurrent information. Boundaries are also associated with updating of the event model, which may trigger consolidation of the previous event and create separation between the previous and new event in memory. These and other boundary-related processes are described in detail in Section 2. Second, during an ongoing event, maintenance of the appropriate event model increases access to relevant information from the past to make predictions about the future (Richmond & Zacks, 2017). This selective availability may enhance integration of the present event with other relevant memories. These and other within-event processes are described in detail in Section 3. The distinction between processes that occur at the boundary versus those that occur within an event provides a useful organizing framework. However, it is important to note that they are not independent processes, and indeed are often examined together. Thus, some studies will be reviewed in multiple sections with a different conceptual focus. Finally, ongoing challenges and possible areas for future research will be discussed in Section 4.

2) Boundary processing

2.1 Encoding of boundary-related information

A key feature of event boundaries is that they are associated with increased uncertainty about what to expect (Zacks et al., 2009, 2011). By definition, encountering a boundary means that the just-active event model has failed to predict one's current situation, so a new event model must be established. In order to update appropriately, information from the new situation must be sampled to determine its identity. Thus, event boundaries may be associated with a transient increase in externally-oriented attention. Supporting this idea, event boundaries have been shown empirically to trigger longer dwell times (Hard et al., 2011), increased visual exploration (Eisenberg & Zacks, 2016) and reduced mind wandering (Faber et al., 2018). Computationally, transient increases in externally-oriented attention can be achieved through an attentional gating mechanism (Reynolds et al., 2007; Zacks et al., 2007). When prediction error is high, the gate

opens and allows the event model to be updated according to the current perceptual input. When prediction error is low, the gate closes such that the event model can be maintained as long as it is making accurate predictions (Figure 2).

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This account of boundary processing suggests that, due to an increase in externally-oriented attention, boundaries should drive memory enhancements specifically for information encountered close to them. In line with this, early work on event segmentation during movie watching indicated that recognition memory for still frames is enhanced when those frames are taken from natural breakpoints (Newtson & Engquist, 1976). Subsequent research using more controlled movie clips has indicated that single objects embedded within complex scenes also tend to be recognized at higher rates when their presence coincides with an event boundary (Swallow et al., 2009). This is true even when those objects are not fixated, consistent with the idea that event boundaries trigger attentional broadening. Data across a range of tasks consistently show enhanced item memory for information encountered near a boundary. In spatial navigation, vivid recollection is more common for locations encountered just before turns, which are thought to induce segmentation (Brunec et al., 2020). In reward learning research, prediction errors, which have been shown to act like boundaries in segmenting memory (Rouhani et al, 2020), also enhance recognition of incidentally associated images (Rouhani et al., 2018, 2020). This memory enhancement is equivalent for positive and negative prediction errors and is independent of reward learning effects, consistent with the error-gated attention proposed by EST rather than mechanisms related to reward per se (c.f., Jang et al, 2020).

Evidence of boundary-related memory enhancements also extends beyond item recognition. For example, in a paradigm in which objects were presented with task-relevant background colors, changes in color were associated with higher object-color associative memory (Heusser et al., 2018). A similar enhancement has been shown for object-tone associations at auditory boundaries, which interestingly also elicit pupil dilation, a marker of autonomic arousal (Clewett et al, 2020). These findings are consistent with the idea that boundaries trigger attentional broadening such that more contextual information is integrated into the memory representation.

Free recall, which is also thought to rely on associative memory processes (Kahana, 1996), may likewise be enhanced for boundary items. A boundary recall advantage has been found in naturalistic navigation (Jeunehomme & D'Argembeau, 2020) and movie viewing (Schwan et al., 2000) tasks, as well as in list recall for words that occur at task-context changes (Polyn et al., 2009).

While memory is typically enhanced for information encountered near a boundary, some free recall studies have not observed a clear benefit for recalling boundary items (e.g., Ezzyat & Davachi, 2011; Heusser et al., 2018). In one movie-viewing study, unedited clips did not show higher recall for boundary information (Gold et al., 2017). However, when boundaries were explicitly cued through editing, they were recalled at higher rates than when other content was cued, suggesting that explicitly orienting to the boundary may be necessary to observe memory benefits. In another investigation, participants encoded information while experiencing different types of boundaries, from changes in one's physical location to situational changes in a narrative (Pettijohn et al., 2016). Recall was consistently higher when the experience included boundaries, but not specifically for information encountered near the boundary. Together, these data suggest that there may be important constraints on when and how memory for boundary information is enhanced and that boundary-triggered modulation of memory may extend into surrounding events.

Neuroimaging data collected during event processing have revealed a broad set of regions engaged at the moment a boundary occurs. In particular, a major focus of the literature is on a set of cortical regions — comprised of the posterior cingulate, precuneus, and retrosplenial cortex — collectively referred to as the posterior medial cortex (PMC). The PMC has consistently been shown to respond to event boundaries in videos (Zacks et al., 2001), written narratives (Ezzyat & Davachi, 2011; Speer et al., 2007), and auditory narratives (Whitney et al., 2009). Across these studies, evoked PMC responses tend to be greater for boundaries that signal a big situational change (coarse-grained boundaries; e.g., arriving at a restaurant to dine with a friend) compared to a small change (fine-grained boundaries; e.g., picking up a fork to take a bite of food). Boundary-evoked responses also tend to be enhanced during overt segmentation, although they are still present during passive viewing (Zacks et al., 2001; Speer et al., 2007). These findings are in line with the idea that the PMC may be involved in the representation and updating of

event models that contain high-level situational information including place, time, characters and goals (Ranganath & Ritchey, 2012).

In addition to cortical activation at event boundaries, researchers have investigated the role of subcortical structures of the mesolimbic dopamine system involved in reward prediction error signaling (Schultz & Dickinson, 2000). In particular, one neuroimaging study using films regularly paused the video to ask viewers to predict what would happen next (Zacks et al., 2011). Behaviorally, prediction accuracy was better within events than at event boundaries, consistent with EST. Targeted fMRI analyses revealed that predictions at boundaries were associated with increased activation in parts of the midbrain and striatum. These findings are consistent with the idea that the mesolimbic dopamine system may play a role in signaling event boundaries, however several processes may be simultaneously engaged (e.g., attentional re-orientating, working memory updating, memory encoding), making it challenging to interpret boundary-evoked activation on its own as a prediction error signal.

Another approach to understanding neural boundary effects on memory is to examine brain regions that specifically promote encoding at boundaries by using a subsequent memory design (Paller & Wagner, 2002). Such investigations have shown that, at the moment a boundary occurs, activation of the lateral prefrontal cortex (PFC) is predictive of later memory for both narrative event boundaries (Ezzyat & Davachi, 2011) and context boundaries (DuBrow & Davachi, 2016). Targeted analyses of the hippocampus have indicated that it may also play a role in the encoding of information around a boundary. In particular, boundary-evoked hippocampal activation has been associated with subsequently being able to correctly recall sequences that spanned the boundary (DuBrow & Davachi, 2016). Several theories might account for this boundary-evoked subsequent memory effect. One possibility is that hippocampal novelty or “mismatch” detection engages dopaminergic midbrain systems (see also, Fernandez et al./Chapter 4.3), which then feed back into the hippocampus to promote integrative encoding across the boundary (Lisman & Grace, 2005; Shohamy & Adcock, 2010). Specifically, when the current event model fails to predict new sensory information at a boundary, a strong mismatch signal may stimulate dopamine release in the hippocampus, which may in turn promote integration of novel information from the new event with the previous event. Alternatively, boundary-triggered hippocampal and lateral prefrontal memory effects may be related to the short-term retrieval or “refreshing” of the just-encountered, preboundary information (Johnson et al., 2005; Öztekin et

al., 2009), which may promote the sequential binding of neighboring events in memory (Clewett et al., 2019). Consistent with the short-term retrieval account, greater activation in the hippocampus, medial temporal lobe (MTL) cortical regions and the PMC has been observed when participants retrieved recently encountered objects that occurred prior to an event boundary (Swallow et al., 2011). Alternative accounts of boundary-evoked memory effects in the hippocampus are further discussed below.

2.2 Boundary-triggered retrospective processing

An emerging theory suggests that hippocampal activation at event boundaries may reflect rapid memory replay of the entire just-experienced event (Ben-Yakov & Dudai, 2011; Griffiths & Fuentemilla, 2020). Replay typically refers to the temporally compressed, sequential reinstatement of hippocampal neural activity elicited during recent experience and is thought to play a key role in long-term memory consolidation (Foster, 2017; see also Kuhl & Zhao/Chapter 5.10 “Content Reinstatement” and Moscovitch & Gilboa/Chapter 6.4 “Consolidation”). While replay was originally detected during sleep (Wilson & McNaughton, 1994), immediate post-experience replay during awake rest has also been consistently observed (e.g., Diba & Buzsáki, 2007; Foster & Wilson, 2006). This has led to the idea that boundaries may serve as brief breakpoints, like post-experience rest, during which hippocampal replay can occur (Bilkey & Jensen, 2019; Clewett & Davachi, 2017).

Scalp electroencephalography (EEG) data in humans have further supported the view that boundaries may serve as replay opportunities. In one study, context shifts were associated with the reinstatement of spatiotemporal EEG patterns from the preceding event during the time window that cellular replay is thought to occur (Sols et al., 2017). Another study demonstrated that when EEG pattern similarity from preboundary to postboundary periods was higher (i.e., consistent with reinstating preboundary information), the preceding event was more likely to be recalled on a later memory test (Silva et al., 2019). Interestingly, boundary-evoked activity was specifically associated with recall of information that came before but not after the boundary, an asymmetry expected from retrospective replay (Figure 3a,b). These EEG data have the temporal precision to identify rapid replay-like events at boundaries, however it is unclear whether these signals are driven by cellular replay in the hippocampus specifically.

Using fMRI, researchers have linked hippocampal activation at boundaries to replay-like processing, but at the slower timescale of the hemodynamic signal. One line of work examining post-stimulus activity has identified a strong and reliable hippocampal response at the end of movie clips that correlates with later memory (Ben-Yakov & Dudai, 2011). This “offset” response has been observed for both isolated film clips as well as clips immediately followed by other unrelated content (Ben-Yakov et al., 2013), suggesting that the response is more likely triggered by the completion of an event (i.e., a boundary) rather than the onset of a rest period. The hippocampal offset response has also been shown to diminish with repeated exposures to the same clip across days (Ben-Yakov et al., 2014), which likely reflects learning of the event model. Thus, later exposures may have lower uncertainty over how and when the event ends, reducing potential mismatch signals as well as the need to engage further memory consolidation mechanisms (e.g., replay) at the end of the event.

Similar responses have also been observed at event boundaries during continuous movie viewing. In one dataset, high-amplitude hippocampal responses reliably predicted boundary locations (Ben-Yakov & Henson, 2018), and those boundary-evoked hippocampal responses were shown to correlate with general memory ability across individuals (Reagh et al, 2020). In a related fMRI study, participants were scanned during both movie viewing and a subsequent recall phase that involved retelling the story from memory (Chen et al., 2017). This design allowed the researchers to link boundary-related processes during encoding (i.e., movie viewing) to retrieval processes. Hippocampal responses to boundaries elicited while watching the movie were shown to correlate with later cortical memory reactivation during the recall phase (Baldassano et al., 2017; Figure 3c). Critically, the relationship between the hippocampal response and reactivation was specific to the event preceding the boundary but not the subsequent event. As with the EEG data described above, this finding is consistent with the idea that boundary-evoked neural activity reflects retrospective memory processing of the just-completed event. Together, the timing of the EEG signals, the localization of the fMRI effects to the hippocampus, and the specific relationship between these neural signals and retrospective memory suggests these effects may be driven by hippocampal replay. However, the mismatch detection and short-term retrieval/refreshing mechanisms discussed above may also play a role.

----- Insert Figure 3 -----

Indeed, it is important to note that replay-like retrospective processing is just one component of a broader set of functions that the hippocampus may play at boundaries. Retrospective processing alone cannot account for observed post-boundary relational memory enhancements (Heusser et al., 2018) or the binding of sequential information across events in memory (DuBrow & Davachi, 2016; Sols et al., 2017). Thus, the hippocampus may play at least two distinct but complimentary roles at event boundaries: 1) at the end of an event, ‘printing’ the just-experienced information into long-term memory via replay, and 2) at the beginning of an event, integrating new sensory information with the previous event to form a coherent sequence (Clewett et al., 2019; Richmond & Zacks, 2017). Griffiths and Fuentemilla (2020) propose that these functions occur during different phases of the theta cycle, which preserves the distinction between the sensory information from the new event and the reactivated trace of the preceding event.

2.3 Segmenting event memories

The key function of an event boundary during online processing is to update the active event model. This updating can have wide-ranging cognitive consequences including enhancing memory for peri-boundary information, as described in the previous sections. Updating can additionally serve the important memory function of separating the new event from the old, that is, segmentation itself. According to EST, when an event model is updated, the previous model becomes deactivated (Zacks et al., 2007). This creates a sudden shift in one’s mental representation (DuBrow et al., 2017), in contrast to the gradual change that characterizes temporal context theory (Howard & Kahana, 2002; see also Howard/Chapter 3.2 “Memory for Time” and Manning/Chapter 5.11 “Context Reinstatement”). Complete resetting prevents the contents of the new event model from being co-active with the contents of the previous event model, which might otherwise linger (e.g., Chan et al., 2017; Ezzyat & Davachi, 2021). By enforcing temporal separation between active event representations, boundaries may prevent interference between nearby events in both working memory and long-term memory (Radvansky & Zacks, 2017).

Evidence that the contents of working memory are reset at event boundaries comes from studies that probe item recognition during continuous event processing. In one series of studies, virtual navigation between different rooms was used to induce spatial event boundaries. When participants encountered a boundary by walking through a doorway, they tended to be slower and less accurate at recognizing previously seen objects, controlling for distance traversed, time passed and even spatial context (Pettijohn & Radvansky, 2016a; Radvansky et al., 2010, 2011; Radvansky & Copeland, 2006). Similar effects have been observed in reading and movie viewing. In reading tasks, recognition of previously encountered items tends to be slower (Zwaan, 1996) and less accurate (Speer & Zacks, 2005) when there is an intervening shift in the narrative time frame (i.e., “a moment later” vs. “an hour later”). In movie viewing, recognition of objects is also slower and less accurate when the intervening delay period contains an event boundary, specifically for objects that were only seen within events (Swallow et al., 2009). Retrieving information across boundaries even at this short timescale has been shown to engage a network of regions associated with episodic memory, including the hippocampus, compared to retrieving information from within the same event (Swallow et al., 2011). This suggests that across-event retrieval places higher demand on episodic memory, consistent with the idea that pre-boundary information is removed from working memory. Oscillatory signals related to the maintenance of multiple items in working memory have also been shown to reset at boundaries (Heusser et al., 2016).

In addition to modulating working memory access, event model updating has consequences for how information is represented in long-term memory, in particular with regard to how within-event versus between-event content is organized. Researchers have developed methods to probe separation between items encountered across different events. One approach used to test for separation in an analogous way to the working memory studies is recognition priming. In recognition priming tasks, participants make memory judgments on a series of items that may be more or less associated in memory. When two items presented consecutively are strongly associated, mnemonic processing of the second item should be faster (i.e., primed). Zwaan (1996) found that sentences that were originally encoded within the same narrative time frame showed more priming than sentences separated by a temporal event boundary. Using a reward manipulation, Rouhani and colleagues (2020) showed that recognition priming occurs across nonadjacent items when they are encoded within the same reward state but not when there is an

intervening high reward prediction error. Applying the same logic to temporal order judgments, DuBrow and Davachi (2013) interleaved recency discrimination trials with recognition probes for items that had been presented in the intervening sequence. When the order of the item pairs was judged correctly, recognition for the intervening items was primed, but only when the sequence did not contain boundaries. These demonstrations of within-event but not between-event priming suggest that items are stored in an associative network clustered by event relatedness and separated by boundaries.

The order in which individuals choose to recall items when unconstrained is another sensitive measure of the associative structure of stored memories (Kahana, 1996; see also Chapters 3.2 “Memory for Time”). Paradigms that use a free recall procedure have shown that boundaries create mnemonic distance between items that were otherwise temporally adjacent. For example, in a study that changed the encoding task midway through a word list, recall transitions were relatively reduced across the task-shift boundaries and enhanced within sequences of the same task (Polyn et al., 2009). In a related study introduced in Section 2.1 that defined events perceptually, recall transitions were found to occur more often from boundary items to nearby within-event items than from preboundary items to nearby across-event items (Heusser et al., 2018). While this pattern could arise from strategically recalling all items within the same event context together, the reduction in across-boundary transitions has also been observed when participants are instructed to recall all items in order from beginning to end (DuBrow & Davachi, 2013). Thus, the tendency to make fewer across-boundary transitions is not likely to be purely strategic, but rather may arise spontaneously due to the underlying structure of the memories.

Recognition priming and spontaneous recall implicitly probe the organization of memory, however humans may also have the ability to consciously access this structure. To this end, researchers have explicitly probed mnemonic separation by directly asking participants to judge the distance or duration between items in memory. Using a subjective distance approach, Ezzyat and Davachi (2014) found that nearby items presented with an intervening scene context boundary were rated as being further apart in memory compared to same-context items, despite the actual distance in trials being matched. This boundary-related separation effect was also associated with hippocampal activation patterns. Specifically, the left hippocampus showed greater pattern change for items subsequently rated as being further apart in the boundary condition. Behaviorally, similar distance effects have been observed for items presented across

large changes in reward value (Rouhani et al., 2020) and across tone changes that induce arousal responses (Clewett et al., 2020). Across longer timescales, Lositsky and colleagues (2016) found that the number of event boundaries encountered while listening to a story correlated with the amount of time participants thought had passed when making retrospective duration judgments. In this case, pattern change in the right entorhinal cortex and ventrolateral PFC was associated with longer remembered duration. Together, these data suggest that we remember experiences that occur across event boundaries as though more time passed between them compared to duration-matched experiences within the same event.

The increased perceived separation between items that span event boundaries has consequences for other forms of memory as well. Temporal order memory, in particular, has been studied extensively in event boundary paradigms. While order memory generally tends to be better when items are objectively further apart (Yntema & Trask, 1963; for review, see Friedman, 1993), the increased subjective distance observed across boundaries has yet to be shown to lead to similar order memory benefits. Instead, sequence and order judgments tend to be more accurate for items within the same event context compared to when they span a boundary (Davachi & DuBrow, 2015). This is likely because multiple mechanisms can support order memory: while increased distance may benefit performance when relying on item memory, inter-item associations are thought to provide the most precise sequence information (DuBrow & Davachi, 2017; Friedman, 1993; Konishi et al., 2006). Boundaries have been shown to disrupt these inter-item associations, thereby reducing accuracy for temporal order judgments (DuBrow & Davachi, 2013, 2014; Rouhani et al., 2020, Figure 4a,b). Similarly, cued recall for the next item in a sequence has been shown to be reduced across both temporal (Ezzyat & Davachi, 2011) and spatial boundaries (Horner et al., 2016). This effect has been specifically linked to boundary-related disruption, as order memory tends to be worse when the intervening boundary has a large response-time cost (Heusser et al., 2018; Figure 4c). Together, these data suggest that a major consequence of segmentation is the greater relative precision of sequential associations between items within the same event as compared to between items that span different events.

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While boundaries create separation in general, individual events do not become completely disconnected from their neighbors. Indeed, as described at the end of Section 2.1, boundary-triggered memory mechanisms may help bind preboundary and postboundary information. Hippocampal and lateral PFC activation at the time of a boundary is associated with subsequent across-boundary recall (DuBrow & Davachi, 2016), and hippocampal pattern similarity across sequences with boundaries is associated with accurate subsequent temporal order memory (DuBrow & Davachi, 2014). Thus, hippocampal and lateral PFC mechanisms may help link neighboring events in the same way that they have been shown to support explicit binding across temporal gaps (Hales et al., 2009; Hales & Brewer, 2010, 2011; Konishi et al., 2006; Staresina & Davachi, 2009). This may occur proactively, by maintaining information across boundaries (e.g., within recurrent loops; Treves & Rolls, 1992; Koster et al., 2018), or retroactively, via the replay mechanisms discussed in Section 2.2 (Griffiths & Fuentemilla, 2020; Sols et al., 2017) or by actively retrieving or “refreshing” preboundary information after a brief delay (Johnson et al., 2005; Öztekin et al., 2009). Thus, segmentation is not necessarily all-or-none (see also Section 4). Instead, processes such as active maintenance or replay that lead to coactivation of preboundary and postboundary information may mitigate some of the downstream consequences of segmentation on memory.

3) Within-event processing

3.1 Maintenance of working memory representations

Event models are thought to facilitate in-the-moment processing because they allow prioritization of the most currently-relevant information (Zacks et al., 2007). One way in which this prioritization may occur is through the selective maintenance of information in working memory. As described in Section 2.3, recognition priming studies have provided evidence that boundaries “reset” the contents of working memory by demonstrating reduced accessibility of items encountered in the previous event compared to the current event (Pettijohn & Radvansky, 2016a; Radvansky et al., 2010, 2011; Radvansky & Copeland, 2006; Swallow et al., 2009, 2011; Zwaan, 1996). These findings suggest that prior event representations that could interfere with the new event are removed from active working memory at boundaries. This reduced access to previous event content can also be described as a relative increase in access to within-event

information. That is, since working memory is capacity-limited (Cowan, 2010), deactivating previous event representations frees more resources to be available for processing current event information (Kurby & Zacks, 2008). This relationship between working memory and event processing is further supported by individual differences data suggesting that, among several constructs of general cognitive ability, working memory capacity is uniquely predictive of segmentation ability (Sargent et al., 2013). One way that greater working memory capacity may support segmentation ability is by allowing greater continued access to relevant content such that the event model can make more accurate predictions and be updated when necessary.

A major finding in the cognitive neuroscience of working memory is that as the number of items or tasks being held in working memory increases, neural activity reflects this increased demand (D'Esposito et al., 1995; Vogel & Machizawa, 2004). Thus, to investigate working memory representations during event processing, researchers have examined whether neural activity increases with the amount of information encountered across an event. In one narrative reading study, brain regions including the ventromedial PFC, middle temporal gyrus and MTL cortex showed linearly increasing activation with each new sentence of the event that was associated with memory for within-event sequences (Ezzyat & Davachi, 2011). In another study discussed in more detail in Section 3.3, event structure was induced by exposing participants to random walks through a stimulus space organized into clusters (Schapiro et al., 2013; Figure 5a). The researchers found that a large set of voxels in the inferior frontal gyrus, a region consistently implicated in working memory maintenance (D'Esposito et al., 1998), positively scaled with the number of stimuli shown within the same event cluster (Figure 5b). These data suggest that as an event model persists, information in working memory accumulates.

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Oscillatory patterns related to maintaining a sequence in working memory over a delay period (e.g., Hsieh et al., 2011) have also been examined to test increasing working memory demands across an event. One magnetoencephalography (MEG) study measured coupling between different frequency bands across events defined by task-relevant background colors (Heusser et al., 2016). According to a prominent model of sequence encoding, individual items may be

represented in successive, fast gamma cycles within a broader, slower theta cycle (Jensen & Lisman, 2005). Theoretically, as more items are added to an event sequence in working memory, more high-amplitude gamma cycles representing those items would be contained within a single theta cycle. Thus, at the beginning of an event, theta-gamma phase-amplitude coupling would be high because only one or two items would be represented by high-amplitude gamma at the early phase of theta. As more and more items are added, increasing high-amplitude gamma at the later phase of theta would reduce the phase-specific relationship. Remarkably, this is exactly what the authors of the MEG study found – across an event, theta-gamma phase-amplitude coupling linearly decreased, and, importantly, this effect was strongest when the sequential order of items was later remembered (Heusser et al., 2016). This cross-frequency coupling may provide a physiological mechanism by which low frequency event processing can shape higher frequency stimulus processing.

3.2 Event schemas and within-event stability

While active working memory maintenance should linearly increase across an event until a capacity limit is reached, event models themselves should theoretically be more stable. This stability is useful in that it allows event representations to be robust to brief disturbances, like occlusion or distraction (Zacks et al., 2007). The gating of bottom-up perceptual input, as described in Section 2.1, and the top-down input from event schemas (or schemata) both contribute to the stability of event models (Figure 2). As briefly introduced in Section 1, event schemas are generalized, semantic representations of event types (Radvansky & Zacks, 2011), typically with a stereotyped sequential structure, or “script” (Schank & Abelson, 1977). In the “ordering food” example, the event schema would consist of the general set of expectations regarding ordering food at a restaurant, including the goal-relevant objects (e.g., menu), characters (e.g., server), and sequence of events (e.g., reading the menu before ordering). When integrated with idiosyncratic, bottom-up perceptual input (e.g., the specific restaurant), they form the current event model.

As shown in Figure 2, information flow between event models and schemas is bidirectional. The influence of event models on event schemas allows updating of the schema based on new experiences. For example, if a restaurant changes their menu to be presented on a tablet, one’s

“ordering food” schema may be broadened to accommodate this new object type, particularly if it is also encountered at other restaurants. In this way, event schemas contain a generalized, long-term record of the past, composed of the common features of events accrued over many prior experiences (Zacks et al., 2007). Thus, the influence of event schemas on event models increases the accessibility of relevant information from long-term memory. This heightened access to long-term memory representations is thought to effectively increase the capacity of event models beyond working memory limits, a construct referred to as “long-term working memory” (Ericsson & Kintsch, 1995). Relatedly, schemas may facilitate processing by rapidly integrating input from the unfolding event into pre-established roles (e.g., the customer or the server) and their relationships, as formalized in a recent computational model of event processing (Franklin et al., 2020).

The stability of events should only be disrupted at event boundaries with the selection of a new event model. Thus, the representational dynamics of event models should show stable states punctuated by brief transition points. This pattern has been identified in the brain in a study using fMRI (Baldassano et al., 2017) and another using EEG (Silva et al., 2019). In both cases, data were collected while individuals watched movies containing natural transitions between scenes. Interestingly, the fMRI study showed that the optimal number of stable states varies across brain regions: low-level regions (e.g., early visual cortex) tended to show rapid switching between stable states, suggesting that they tracked fine-grained perceptual boundaries, whereas higher-level regions (e.g., angular gyrus, PMC) showed slower switching (Baldassano et al., 2017). The PMC, in particular, tended to reflect the transition structure identified by humans as meaningful events, suggesting that it may be sensitive to cognitive event models or schemas. In addition, both studies showed that higher-level states identified during movie watching were reactivated during free recall, supporting the idea that abstract event models are central to how events are remembered (Radvansky & Zacks, 2011).

In addition to stability *within* regions during event processing, interactions *between* regions may be important for integrating information from the internal event model with sensory input. Indeed, in a study of sequential recall of lists that contained context boundaries, successful encoding of within-event associations was related to coupling between regions but not with univariate activation in any single region (DuBrow & Davachi, 2016). In particular, the ventromedial prefrontal cortex (vmPFC) showed higher correlations with the hippocampus for

pairs of items within the same event that would later be correctly recalled in sequence. A similar interaction has been observed between the vmPFC and hippocampal pattern stability within, but not between, events (Ezzyat & Davachi, 2021). The vmPFC has been implicated in instantiating and integrating new information into established schemas (Gilboa & Marlatte, 2017; Robin & Moscovitch, 2017), and has been shown to represent schematic information in the context of coherent, temporally-extended events (Baldassano et al., 2018). Thus, coupling between the hippocampus and vmPFC during event processing may support this rapid assimilation of new information into prior knowledge structures (Gilboa & Marlatte, 2017; Preston & Eichenbaum, 2013; c.f., van Kesteren et al., 2012).

It is also important to note that the vmPFC and PMC are just two components of a broader posterior medial network that may support the construction and context-appropriate use of event models (Ranganath & Ritchey, 2012). Regions in this network, which overlap with the default mode network (Raichle, 2015), have been shown to integrate information over the long timescales that event models often operate (Hasson et al., 2015) and are sensitive to differences in high-level schemas even when perceptual input is matched (Yeshurun et al., 2017). The posterior medial network may also be involved in learning new schemas. In one study, repeatedly presenting isolated movie clips in a nonsensical but fixed sequence was associated with increased coupling between nodes of the network (Aly et al., 2018). Thus, in addition to schema processing, the posterior medial network may also be involved in constructing event schemas from more basic elements (e.g., isolated movie clips) when they demonstrate reliable temporal structure. Indeed, event schemas may emerge from the ability to detect structure in abstract events (Hard et al., 2006).

3.3 Prediction and learning

As proposed by EST, the major adaptive function of event segmentation is the generation of predictions that anticipate what will happen next (Kurby & Zacks, 2008; Richmond & Zacks, 2017). Engaging an event model that closely matches the current situation facilitates the processing of event-consistent (i.e., predicted) information. A widely-accepted method for testing whether processing is facilitated within events is to simply measure processing time. In reading tasks, this can be indexed by the time a reader takes before indicating they are ready for

new content. Across many studies, reading times have been shown to be faster within events defined by temporal continuity (Radvansky & Copeland, 2010; Rinck & Weber, 2003; Speer & Zacks, 2005; Zwaan, 1996; Zwaan, Magliano, et al., 1995; c.f. McNerney et al., 2011) and other situational factors (McNerney et al., 2011; Rinck & Weber, 2003; Zacks et al., 2009; Zwaan, Magliano, et al., 1995; Zwaan & Radvansky, 1998). This benefit for within-event reading times is thought to be supported by the increased predictability provided by a well-suited mental model, an idea that has been tested empirically using explicit prediction tasks. In one study, movie viewers were asked to predict what would be on the screen in the near future, and were shown to be more accurate when there was no intervening event boundary (Zacks et al., 2011). In other studies, higher subjective expectedness and predictability ratings have been shown to be directly related to faster reading times (Pettijohn & Radvansky, 2016b; Zacks et al., 2009).

A related approach called the ‘dwell-time paradigm’ measures processing time for nonverbal narrative content by using slideshows, which allow individuals to control how long each image is viewed (see Baldwin & Kosie, 2020 for review). The idea is that if an image requires more processing, the viewer will choose to dwell on it longer before moving on to the next image. Researchers can then compare an image’s average dwell time to how often the image is labeled an event boundary. The original study to use this approach showed that depictions of within-event actions were viewed for less time than boundary actions (Hard et al., 2011). Importantly, this effect was attenuated when predictability was lowered by scrambling the image order. More recent studies have built on this by showing that familiarization with the sequence, which is necessary for accurate prediction, increases the dwell time difference between within-event and boundary images (Hard et al., 2019; Kosie & Baldwin, 2019). Together, the dwell time and reading time data support the idea that the generally high predictability within events reduces cognitive demands relative to boundaries.

How then do we acquire the knowledge about events that allow us to predict what will happen next? One key mechanism is statistical learning (see also, McClelland & Botvinick/Chapter 2.3). During early learning, in the absence of prior event knowledge, segmentation and event learning are mutually dependent – without segmentation, there would be no discrete events to learn about, and without event structure, there would be nothing to segment. Decades of developmental research has indicated that, from a very young age, humans can parse continuous stimuli according to statistical regularities in speech (Aslin et al., 1998; Saffran et al., 1996), action

sequences (Baldwin et al., 2008; Saylor et al., 2007), and other modalities (for review, see Aslin, 2017; Turk-Browne, 2012). This statistical learning inherently segments experience and may be a first step towards building more complex event structures (Levine et al., 2019).

Statistical learning typically relies on differences in transition probabilities such that predictability is high within events and uncertainty increases at event transitions (e.g., Saffran et al., 1996). Increased uncertainty or prediction error is useful in this context for determining when an event starts and ends (Reynolds et al., 2007), but sequential predictability may be less useful for learning rich, within-event structure (Zacks et al., 2001). If learning required every within-event transition to have a high probability of occurrence, within-event representations would become largely inflexible. In the “ordering food” example, the customer would always have to order a drink before an appetizer, an appetizer before an entrée and so on; if anything was out of order, prediction error would trigger event segmentation inappropriately. This sort of rigidity may be important for learning that involves fixed relationships, e.g., learning the order of phonemes that form a word. However, it is incongruent with the EST conceptualization that events are made up of hierarchically-organized parts that may be flexibly accessed (Zacks et al., 2007; Zacks & Tversky, 2001).

One way in which researchers have begun to study the learning of more flexible event representations is by exposing participants to random walks through a stimulus space organized into clusters, as briefly introduced in Section 3.1 (Schapiro et al., 2013). In the diagram shown in Figure 5a, each node of the network represents a stimulus. Each stimulus is connected to four others by a line, indicating a fixed transition probability between them. Although the individual transition probabilities are matched, the structure of interconnectedness gives rise to three clusters shown in different colors. Each cluster can be conceptualized as a very simple event model where a node is a component of the event (e.g., the menu in the “ordering food” example). In the experiment, participants saw sequences of stimuli that corresponded to random trajectories through the network. After being exposed to these sequences, participants were able to identify the boundaries between the three clusters despite having no additional cluster information (Figure 5c). This clustering was reflected in patterns of activation in the bilateral hippocampus, left lateral PFC, and parts of the left temporal lobe (Schapiro et al., 2013, 2015; Figure 5d). These findings suggest the brain can rapidly extract higher-order relationships even in the absence of lower-level differences in transition probability. Learning of higher-order

relationships that unfold over time has been successfully modeled with recurrent neural networks (Elman & McClelland, 1997; Franklin et al., 2020; Reynolds et al., 2007; Schapiro et al., 2013), which may provide a good model of event schemas because of their ability to capture dynamics and generalize across specific instances.

4) Ongoing challenges

In the real world, events are rarely perfectly delineated. For example, when you finish ordering food and your menu is taken away, the server leaves but your dining companion remains. Even if the characters change between these events, physiological signals (e.g., hunger) may persist and the broad spatiotemporal context (e.g., evening at the restaurant) remains the same. Research has shown that, while memory access for objects is generally reduced across spatial boundaries, there is some savings in accuracy and response times when the objects are carried across boundaries (Radvansky & Copeland, 2006). This suggests that event representations may be updated in a continuous manner along multiple dimensions (e.g., space, characters, objects) separately (Zwaan, Langston, et al., 1995). Continuous change that occurs along multiple dimensions and/or with uncertainty presents a major challenge for the all-or-none segmentation proposed by EST, which requires complete replacement of the active event model at a specific moment in time (i.e., global updating). A second major challenge for the theory is determining at what temporal resolution, or multiple resolutions, to segment experience. These and related issues are discussed below, but note they represent just a subset of the many outstanding questions being actively addressed in the field.

The first challenge has been referred to as the “fuzzy boundary” problem (Zacks et al., 2007). In everyday experience, it can be difficult to identify precisely when one event ends and another begins. Because perceptual change often occurs gradually, large and abrupt sensory prediction errors can be exceedingly rare. Boundaries may even occur without any change in sensory input, as when context shifts are internally cued (see DuBrow et al., 2017 for review). Thus, rather than mapping sensory observations directly to segmentation, an intermediate inference process that identifies the underlying cause of the observations may be key for optimizing segmentation (Shin & DuBrow, 2020). For example, when ordering food, the menu may be taken away because you are done ordering or because you were given the wrong menu. Despite the sensory information

being the same, event model updating should only occur in the former case, while the “ordering food” event model should persist in the latter. Thus, triggering segmentation based on the underlying cause of the observed change instead of the observed change itself may help better identify moments when it is or is not appropriate to update.

The fuzzy boundary problem is compounded by the idea that segmentation involves a complete resetting of the active event model. As discussed in Section 2.3, a key assumption in EST is that when one event ends, a completely new event begins (Zacks et al., 2007). This can be a useful simplifying assumption, because it allows only one event model to be engaged at a time, and minimizes the opportunities for updating (i.e., engaging in a demanding selection process) to just the brief moments surrounding a boundary. However, real-world events may not always be so well delineated. For example, a conversation that started over dinner at a restaurant may continue into your car ride home. Global updating upon leaving the restaurant would impair your ability to carry on the conversation coherently, yet it may still be appropriate to segment because different behaviors are associated with restaurants and car rides. Rather than all-or-none segmentation, allowing for multiple “threads” might provide a better solution, at least in some cases. In the prior example, the restaurant thread could be replaced by the car ride thread, while allowing the conversation thread to continue. Narrative comprehension studies have shown evidence for both types of updating -- global updating even when only a single dimension changes, and incremental updating of individual threads (Bailey & Zacks, 2015; Curiel & Radvansky, 2014; Kurby & Zacks, 2012). Both may be important mechanisms for event processing, but further work is needed to determine when global versus incremental updating occurs and how multiple event models might co-exist.

One idea that starts to address how multiple event streams can be maintained simultaneously is hierarchical event models. Indeed, a theory of event hierarchy may solve the second major challenge of segmentation described above -- determining the appropriate temporal resolution -- by suggesting that multiple levels can be tracked in parallel (Zacks et al., 2007). That is, segmentation may simultaneously occur at a coarse level, as in arriving at and then leaving a restaurant, at a very fine level, as in picking up a fork and then moving it to one’s plate, and at intermediate levels, as in ordering food and then returning to one’s prior conversation. Behavioral experiments in which participants are asked to indicate when a boundary occurs have demonstrated that people can alter their resolution in a goal-directed manner (Newtson, 1973;

Zacks et al., 2001). Interestingly, neural (e.g., Speer et al., 2007) and viewing time (e.g., Kosie & Baldwin, 2019) correlates of segmentation are enhanced at coarse event boundaries, suggesting that there may be a preferred, natural level of segmentation (Zacks & Tversky, 2001). Indeed, the natural resolution of segmentation, which varies across experiences and individuals, may play a particularly important role in determining the fidelity of memory representations (Jeunehomme & D'Argembeau, 2020).

In sum, a wealth of data indicates that in-the-moment event processing has a major influence on the structure of memory, yet many open questions remain. Simultaneously tracking events at multiple resolutions remains an ongoing challenge. If events are organized hierarchically in memory as well as in perception, this may have important consequences for how memories are sampled during retrieval (Shin & DuBrow, 2020) and whether interference occurs (Radvansky & Zacks, 2017). Temporal hierarchies may also be a fundamental property of our cortical circuits (Hasson et al., 2015) related to segmentation granularity (Baldassano et al., 2017). Yet, how these neural systems may give rise to segmentation and memory behavior remains unclear. An emerging theory proposes that the long-axis of the hippocampus itself may represent a hierarchical gradient (Brunec et al., 2018; Collin et al., 2017; Poppenk et al., 2013), further underscoring the relationship between event hierarchies and memory. Still, even if multiple temporal resolutions of segmentation can be tracked hierarchically, the natural resolution of segmentation may play a special role in organizing memory. Future work addressing these fundamental questions about event processing will help to further characterize the relationship between event segmentation and memory.

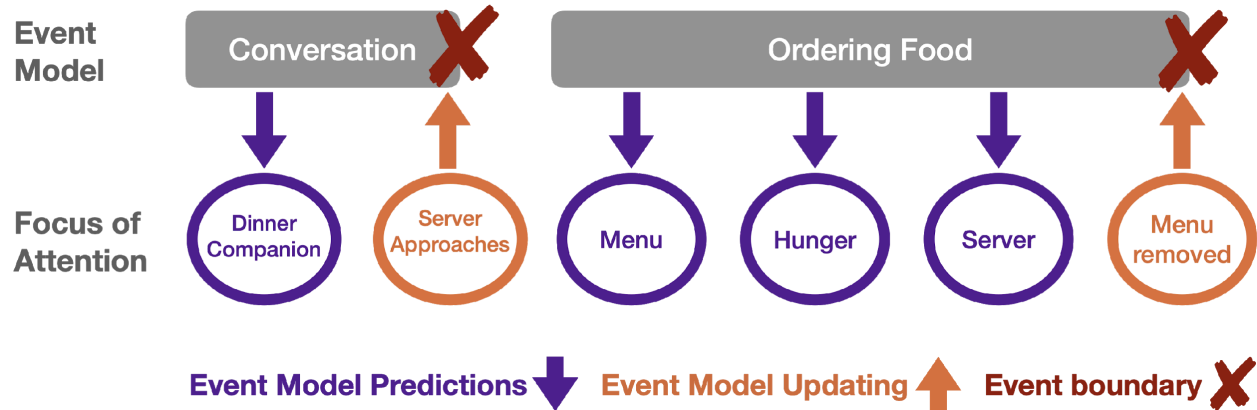


Figure 1. Example of event segmentation at a restaurant. The first event model reflects the conversation one is having with their dinner companion at a table before having ordered food. The focus of attention is on the dinner companion, and this sensory input is perfectly predicted by the “conversation” event model. As the server approaches, attention is shifted away from the dinner companion towards the server. This sensory input is inconsistent with the active event model and therefore triggers an event boundary. Event model updating occurs as information is gathered about the new event. Once it is clear that the server is there to take the diners’ orders, the “ordering food” event model is engaged. Looking over the menu, introspecting about one’s hunger level, and interacting with the server are all predicted by the active model, which remains active so long as these predictions are met. Because “ordering food” involves looking at the menu, when the server takes away the menu, another event boundary is triggered.

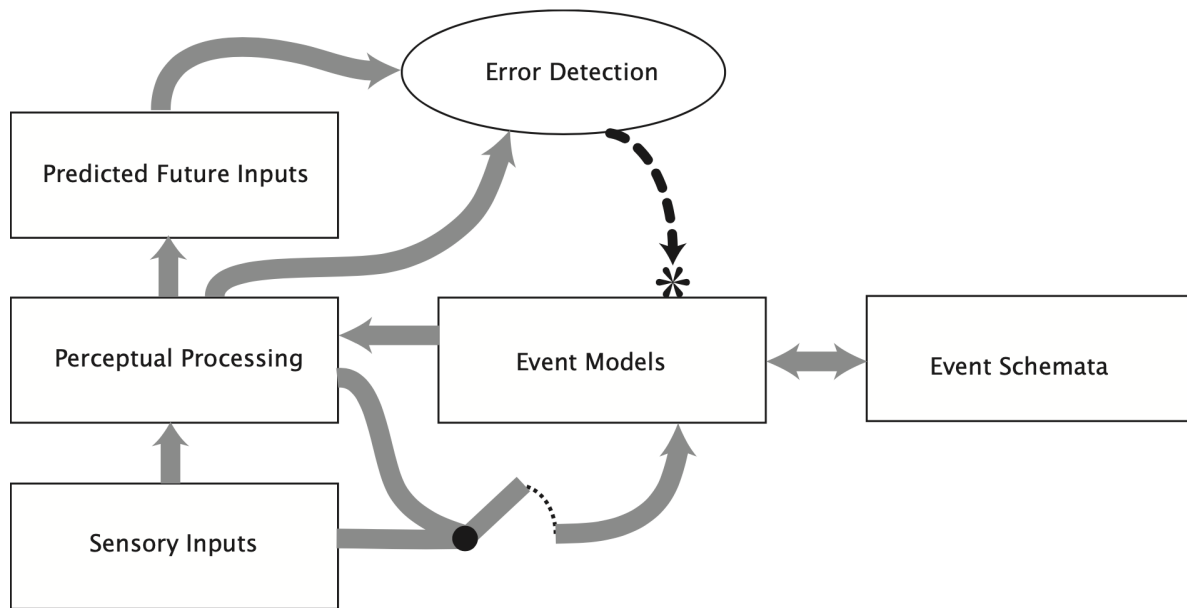


Figure 2. Schematic depiction of Event Segmentation Theory from Zacks et al. (2007). Grey arrows represent information flow. The connection from sensory inputs/perceptual processing to the event model is gated by error detection. When predictions are accurate (no error detection), sensory inputs/perceptual processing is blocked from reaching the event model, allowing the event model to remain stable. When predictions are inaccurate (error detection), the event model is reset (dashed arrow) and new sensory/perceptual information propagates to, and updates, the event model.

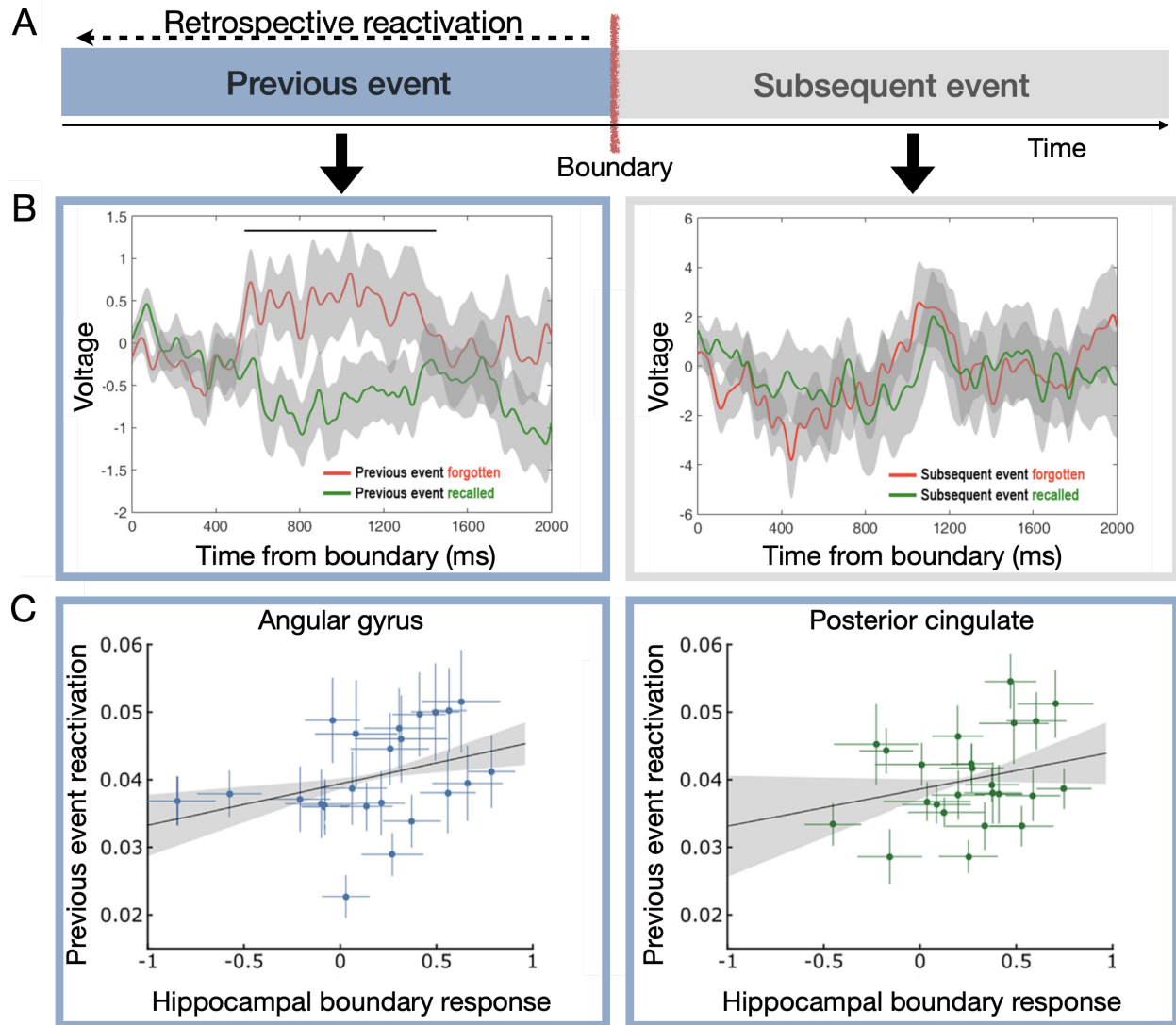


Figure 3. Boundary-evoked retrospective processing. A) Schematic depiction of boundary-triggered retrospective memory reactivation. In this scenario, neural activity evoked at the boundary represents reactivation and/or replay of the preceding event, which may strengthen the memory trace. B) EEG data from Silva et al. (2019). Data represent event-related potentials triggered by boundaries during movie viewing. Green lines represent subsequently recalled events, red lines represent forgotten events, and black lines indicate where they significantly differ. The relationship with memory is shown for both the event preceding the boundary (left) and for the event following the boundary (right). Boundary-evoked activity was related to subsequent recall of the previous event but not the subsequent event. C) fMRI data from Baldassano et al. (2017). Graphs depict the relationship between the hippocampal response during movie viewing on the x-axis and cortical reinstatement during subsequent recall on the y-axis. The hippocampal boundary response was associated with cortical reinstatement of the event preceding the boundary in both the angular gyrus (left) and the posterior cingulate (right).

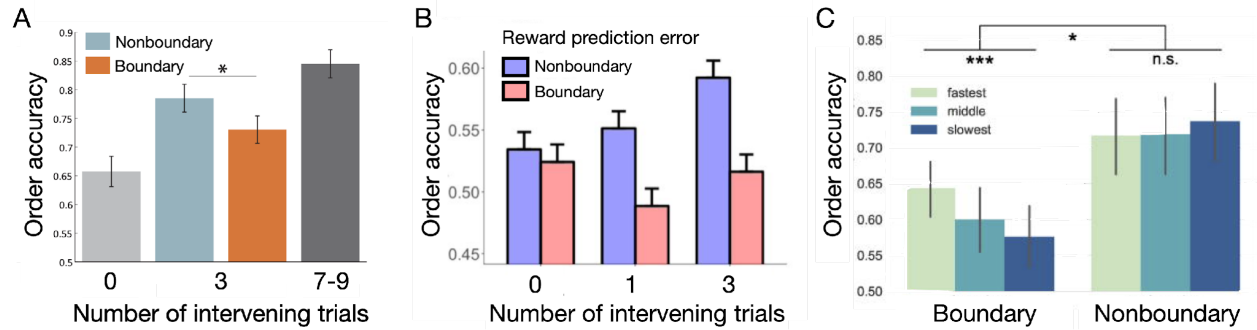


Figure 4. Effects of event segmentation on temporal order memory. A) Temporal order memory judgments from Experiment 1 of DuBrow & Davachi (2014). Accuracy on recency discrimination (“which was more recent” increased with the number of intervening items between image pairs. For image pairs matched for distance (3 intervening items) and category/task context, accuracy was reduced for images that spanned context boundaries. B) Temporal order memory judgements from Experiment 4 of Rouhani et al. (2020). Accuracy on “which came first?” judgments scaled with the number of intervening items when reward prediction error was low (nonboundary) but not when there was a high reward prediction error (boundary). Overall, accuracy was higher for image pairs in the same reward state (nonboundary) than different reward states (boundary), an effect driven by images that spanned but did not include the reward prediction error boundary (1 and 3 intervening items). C) Temporal order memory judgments from Experiment 2 of Heusser et al. (2018). All image pairs spanned 3 intervening items. Accuracy on “which came first?” judgments was reduced for image pairs that spanned a task-relevant perceptual boundary. Boundary-related processing costs were measured by response times at the boundary during encoding and grouped into terciles. Accuracy on the temporal order judgment decreased as a function of response time costs at the boundary but not for nonboundaries.

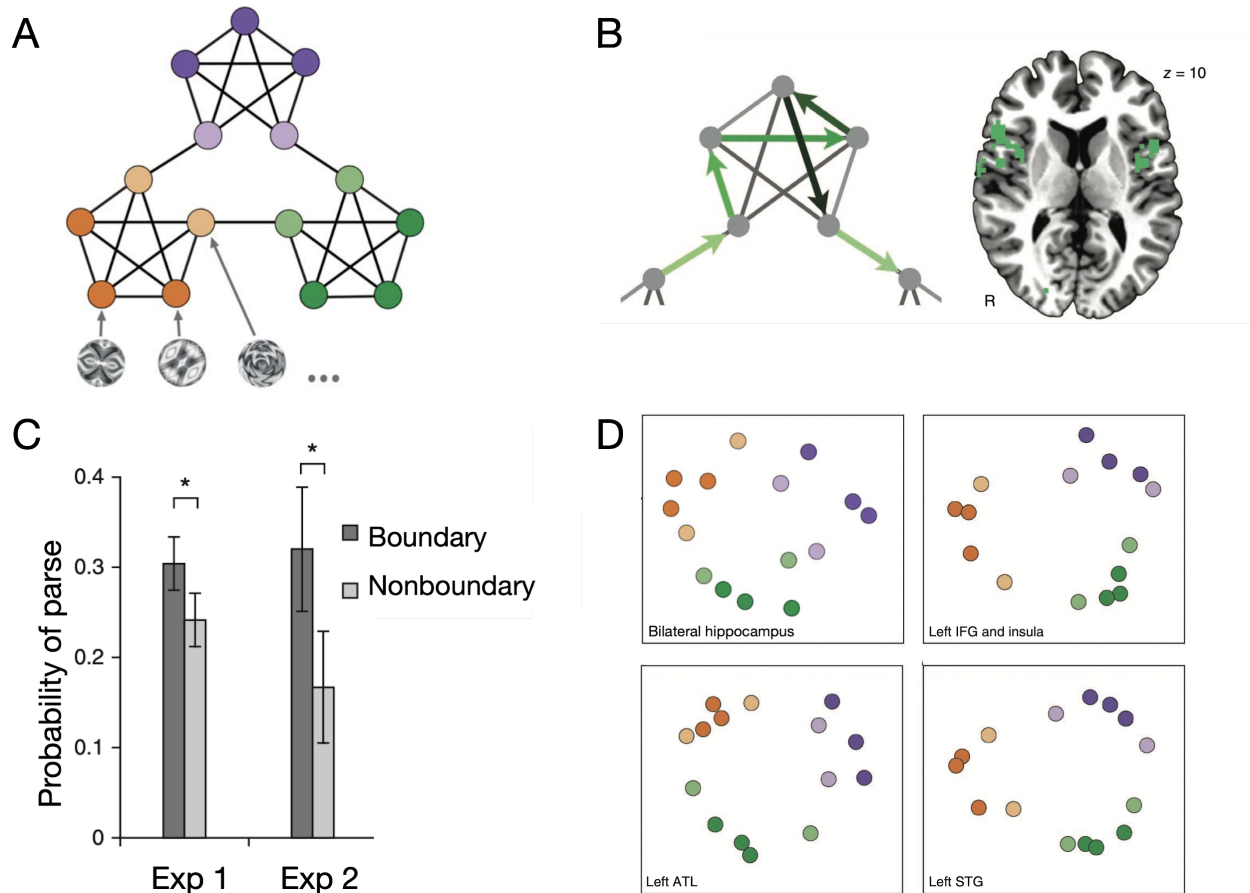


Figure 5. Learning event representations from Schapiro et al. (2013, 2015). **A)** Network organized into clusters used to generate stimulus sequences. Each node represents a stimulus. Example abstract shape stimuli are shown below the network graph. Each line connecting the nodes represents possible transitions of equal probability. The three colors represent three different clusters, where lighter colors reflect boundary items from which transitions to other clusters could occur. **B)** Lighter to darker shades of green represent increasing activation with the number of items presented in the same cluster (left). A regression analysis was run on the fMRI data to identify voxels showing this pattern. Bilateral IFG and insula were found to show increasing activation as more items from the same cluster were viewed (right). This pattern is consistent with an increase in working memory across the event (cluster). **C)** After exposure to stimulus sequences, participants were asked to identify natural breakpoints. Across two experiments, participants were significantly more likely to identify breakpoints at transitions into a new cluster (boundary) than other points in the sequence (nonboundary). **D)** Results of an fMRI pattern similarity searchlight analysis. Brain regions were identified that showed higher correlations (similarity) between patterns elicited by item pairs within the same cluster than item pairs belonging to different clusters. This similarity structure is visualized here with multi-dimensional scaling. The closeness of each pair of nodes represents their average similarity across subjects for each region. Clockwise from the top-right: left inferior frontal gyrus (IFG) and insula, superior temporal gyrus (STG), and anterior temporal lobe (ATL) showed this pattern (Schapiro et al., 2013). Top-left: A reanalysis of the data also revealed this pattern in bilateral hippocampus (Schapiro et al., 2015).

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