



# Event conjunction: How the hippocampus integrates episodic memories across event boundaries

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## Abstract

Our lives are a continuous stream of experience. Our episodic memories on the other hand have a definitive beginning, middle, and end. Theories of event segmentation suggest that salient changes in our environment produce event boundaries which partition the past from the present and, as a result, produce discretized memories. However, event boundaries cannot completely discretize two memories; any shared conceptual link will lead to the rapid integration of these memories. Here, we present a new framework inspired by electrophysiological research that resolves this apparent contradiction. At its heart, the framework proposes that hippocampal theta-gamma coupling maintains a highly abstract model of an ongoing event and serves to encode this model as an episodic memory. When a second but related event begins, this theta-gamma model is rapidly reconstructed within the hippocampus where new details of the second event can be appended to the existing event model. The event conjunction framework is the first electrophysiological explanation of how event memories can be formed at, and integrated across, event boundaries.

## KEYWORDS

episodic memory, event segmentation, memory integration, neural oscillations, theta-gamma coupling

## 1 | EPISODIC MEMORIES ARE FORMED AT EVENT BOUNDARIES

Life is a continuous stream of experience. Episodic memories, however, are discretized short stories of our personal past, anchored to a singular point in time and space (Tulving, 2002). Somewhere between forming and retrieving these memories, therefore, a process must arise to carve unique memories from our stream of consciousness. Numerous cognitive theories have set out to address this very question. Event segmentation theories (Radvansky, 2012; Zacks & Swallow, 2007) state that when a salient change in environment occurs, an *event boundary* is created. The event boundary is thought to segregate the past and present, and induce a rapid and retroactive encoding of experience prior to the boundary to produce a discretized

episodic memory (Radvansky & Zacks, 2017). In contrast, other accounts suggest that elements of an event are proactively encoded during the course of an event through shared contextual links (Clewett, Dubrow, & Davachi, 2019; Schapiro, Rogers, Cordova, Turk-Browne, & Botvinick, 2013). These accounts postulate that when an event boundary is encountered, the boundary produces a large contextual shift that prevents linking between elements of the new event and those of the previous event. While the proactive and retroactive accounts of event memory formation have their differences, they agree that the discretization of event memories (a) occurs during encoding and (b) hinges upon the presence of event boundaries.

Event boundaries can take many forms, including temporal boundaries (DuBrow & Davachi, 2013, 2016; Ezzyat & Davachi, 2011), spatial boundaries (Homer, Bisby, Wang, Bogus, & Burgess, 2016), and

goal-related boundaries (Speer, Zacks, & Reynolds, 2007; Zacks et al., 2001). Importantly, all these forms of boundary exert influence over episodic memory. For example, Horner et al. (2016) asked participants to navigate a series of virtual rooms, each of which contained multiple objects. Later, the participants were asked to recall sequences of objects that were presented within either a single room (where there was no event boundary) or across two rooms (where the door introduces a spatial boundary into the sequence; Radvansky & Copeland, 2006). Participants showed a significant impairment when trying to recall object sequences that crossed into a second room relative to sequences contained within one room. These results suggest that episodic memory is organized in accordance with the spatial boundaries that participants encountered. Ezzyat and Davachi (2011) conceptually replicated this effect using temporal boundaries (that is, time jumps in short narratives) in place of spatial boundaries, suggesting episodic memory can also be organized in accordance with temporal boundaries. Interestingly, individuals who are more effective at segmenting events also recall many more details about these events, even after controlling for a variety of cognitive and demographic confounds (Sargent et al., 2013). As such, it seems that the presence and detection of event boundaries is critical to the successful formation of episodic memories.

On a neuroanatomical level, event segmentation employs a hierarchical network to detect event boundaries (Baldassano et al., 2017); low-level sensory regions are sensitive to fine-grained changes in events while high-level multimodal regions detect coarse and abstract shifts. In one of the first neuroimaging studies of event segmentation, Zacks et al. (2001) time-locked functional magnetic resonance imaging (fMRI) data to event boundaries present in video clips that depicted everyday tasks. Analysis revealed a strong increase in the activity of the posterior medial cortex at these boundaries relative to epochs just before these boundaries. Speer et al. (2007) conducted a similar study where narrative boundaries were used in place of perceptual boundaries and they too found boundary-related neural activity in the posterior medial cortex (mostly greatly in the precuneus). Notably, activation in the precuneus was greater for coarse event boundaries (i.e., great shifts in environment) relative to fine-grained event boundaries (e.g., minor changes in an ongoing task). Further elaborating upon this apparent selectivity to coarse boundaries, Baldassano et al. (2017) built a hierarchical model of event structure using multivariate pattern analysis. They demonstrated that areas in the posterior medial cortex are responsive to multimodal, abstract boundaries (corroborating the findings of Speer and colleagues), while sensory regions (such as the early visual cortex) are more responsive to fine-grained boundaries. Together, these experiments provide strong support to suggest that the brain can detect event boundaries through a hierarchical network. How, though, does the brain use these boundaries to form an event memory?

To form an event memory, all constituent elements of an event need to be bound together to form a coherent representation. The hierarchical network aids in the detection of event boundaries that define where an event begins and ends, but the network does not aid in the association of elements within the event. Rather, this task is thought to fall on the hippocampus (Konkel & Cohen, 2009; Olsen, Moses, Riggs, & Ryan, 2012; Wallenstein, Eichenbaum, & Hasselmo, 1998). Numerous

studies indicate that the hippocampus is a relational hub that associates distinct, abstract concepts (Davachi, 2006; Staresina & Davachi, 2009). *Pattern separation* is thought to accomplish this (e.g., Hunsaker & Kesner, 2013; Rolls, 2010, 2016). Under this framework, the dentate gyrus of the hippocampus orthogonalizes overlapping representational patterns of incoming stimuli, and then recurrent collaterals within the hippocampal subfield CA3 associate these orthogonalized patterns together. Intriguingly, the recurrent collaterals within CA3 may not only facilitate instantaneous binding, but also provide a mechanism to maintain information for binding with other details that become prominent at a later point in time (Gilbert & Kesner, 2006). In line with this idea, several studies have implicated the human hippocampus in the maintenance of recently encountered stimuli (Axmacher et al., 2010; Piekema, Kessels, Mars, Petersson, & Fernandez, 2006). Weaving these strands together, one can speculate that the hippocampus creates a model of an ongoing event (Milivojevic, Varadinov, Vicente Grabovetsky, Collin, & Doeller, 2016) by disentangling overlapping elements of an event through pattern separation (Hunsaker & Kesner, 2013; Rolls, 2010, 2016), maintaining these discrete elements for the duration of the event (e.g., Axmacher, Henseler, et al., 2010), and subsequently, binding these elements together into a coherent event representation (Schapiro, Turk-Browne, Norman, & Botvinick, 2016; Staresina & Davachi, 2009).

Beyond forming and maintaining relational links, a cornucopia of studies have demonstrated that the hippocampus plays a critical role in the formation of episodic memories (e.g., Corkin, 2002; Davachi, 2006; Giovanello, Schnyer, & Verfaellie, 2009; Nyhus & Curran, 2010). As such, one could further speculate that the hippocampus is pivotal in transforming the aforementioned event models into an episodic memory. In line with this idea, Ben-Yakov and Dudai (2011) demonstrated that hippocampal activity spikes at an event boundary (similarly found in Baldassano et al., 2017) to a substantially greater degree when the event is successfully encoded relative to when it is later forgotten, indicating that this boundary response is linked to memory formation. A number of control analyses concluded that this effect was specific to the boundary induced by video offset, rather than video duration or the contents of the videos. The authors speculate that these responses reflect the rapid replay of the event to solidify its memory trace. In line with this idea, two EEG studies (Silva, Baldassano, & Fuentemilla, 2019; Sols, DuBrow, Davachi, & Fuentemilla, 2017) found that neural patterns relating to an event are replayed within a second of encountering an event boundary, and that this replay is predictive of later memory. Whether this replay originates from the hippocampus (as in rodents; Carr, Jadhav, & Frank, 2011), however, is an open question.

In sum, there is strong evidence to suggest that event boundaries serve to segregate the past and present, and create discrete episodic memories. While a large hierarchical network appears to be involved in the processing of event boundaries, it seems that the hippocampus is best suited for the maintenance of the event model, and the transference of this model to episodic memory. It is worth noting, however, that the idea that event boundaries provide a definitive start and end of a memory does not easily reconcile with decades of research into reconsolidation, memory integration and retrieval-induced learning—all of which show that episodic memories are malleable and subject to

updating based on later information. In the next section, we dig deeper into these apparent contradictions.

## 2 | EPISODIC MEMORIES ARE INTEGRATED ACROSS EVENT BOUNDARIES

If two events separated in time-share a common goal or location, what happens to the two event memories? Evidence suggests they become linked in such a way that the retrieval of one brings the other to the forefront of memory (e.g., Griffiths, Mazaheri, Debener, & Hanslmayr, 2016; Miller et al., 2013). Can it really be concluded, therefore, that episodic memories are definitively orthogonalized by event boundaries? Here, we discuss how temporally discontinuous events, separated by event boundaries, have the potential to be fused together.

If two memories share a commonality, they can become integrated. This has been widely demonstrated in associative inference paradigms, where participants are presented with stimulus pairs AB and BC and then probed to see if they can make an inferential link between A and C (which have never been presented together). Any knowledge of link between A and C would suggest that the distinct memory traces AB and BC have become integrated. Evidence suggests humans are remarkably adept at such inferential tasks (e.g., Backus, Schoffelen, Szabényi, Hanslmayr, & Doeller, 2016; Schlichting, Zeithamova, & Preston, 2014; Tomparý & Davachi, 2017; Zeithamova, Dominick, & Preston, 2012). How two memories become integrated, however, is still open to debate. Some theories propose that integration occurs during the encoding of the second memory (i.e., integrative encoding; Nadel, Hupbach, Gomez, & Newman-Smith, 2012; Sekeres, Winocur, & Moscovitch, 2018), while others propose that integration occurs during consolidation or retrieval (i.e., offline integration; Polyn, Norman, & Kahana, 2009; Tomparý & Davachi, 2017). These processes are not mutually exclusive however, meaning memory integration could theoretically occur both during encoding and during offline periods (Zeithamova & Preston, 2010). Here, we concern ourselves with integrative encoding (for further details on offline integration and event memories, see Clewett et al., 2019).

On a neural level, memory integration has been proposed to rely on the coordinated activity of the hippocampus and the medial prefrontal cortex (mPFC; Schlichting & Preston, 2015). In this division of labor, the hippocampus is thought to encode details of unfolding events and reactivate details of past events, while the mPFC is thought to find commonalities across episodes and bias hippocampal reactivation towards relevant past events (Preston & Eichenbaum, 2013). In line with these predictions, patients with lesions to either the mPFC (Spalding et al., 2018) or the hippocampus (Pajkert et al., 2017) suffer deficits in the memory integration that cannot be explained by deficits in associative memory alone. As the nature of these lesions did not change between encoding and inference, however, these studies do not clarify whether these regions specifically impair integrative encoding. To address this, Schlichting et al. (2014) contrasted hippocampal activation during associative encoding (i.e., the first pair; AB) and integrative encoding (i.e., the second pair; BC, where integration of

A and C can occur). They observed a spike in hippocampal activity during successful integrative encoding relative to successful associative encoding, indicating that the hippocampus plays a role in the online integration of episodic memories. Taking a similar approach to MEG, Backus et al. (2016) produced complementary results indicating that an increase in hippocampal neural activity is predictive of integration. Moreover, Backus and colleagues also uncovered evidence to suggest that connectivity increases between the hippocampus and medial prefrontal cortex (mPFC) during online integration, supporting the idea that a hippocampal-mPFC circuit underpins the online integration of distinct episodic memories.

The mechanistic interpretation of these two results remains an open question however. Under the framework proposed by Schlichting and Preston (2015), one would speculate that the hippocampal-mPFC connectivity reflects the directed reactivation of the original pair. This process would be reminiscent of *pattern completion*, where a partial cue reactivates the entire hippocampal memory trace embedded in the recurrent collaterals of CA3. However, the hippocampal activation may also reflect representational binding between the first and second pairs (Davachi, 2006; Staresina & Davachi, 2009). This process would be reminiscent of pattern separation, as described in the previous section. Conceivably, a balance between pattern separation and pattern completion may be optimal for memory integration. Explicitly put, a partial cue (stimulus B of pair BC) would lead to both pattern completion (reinstating the missing stimulus A) and pattern separation (disentangling the B and C). Pattern completion would allow stimulus A to be reinstated in the neocortex and cycled back to the hippocampus by the so-called big-loop (Koster et al., 2018). Pattern separation would disentangle stimulus B and C (and later, the recycled stimulus A) and then bind their hippocampal representations together via the recurrent collaterals of CA3.

Applying the principles of pattern separation and pattern completion go some way to explaining how memory integration can occur during the encoding of the second pair. However, this explanation is imperfect. The hippocampus would need to expose stimulus B to both pattern separation and pattern completion for integration to occur. While we have speculated on how the two processes may interact in the paragraph above, the exact process in which this balance could be achieved is unclear. Moreover, the pattern separation/completion account provides no apparent limiter on the size of an integrated memory. In other words, a seemingly infinite number of memories could be reactivated and integrated with current experience so long as there is a partial cue to pattern complete each of these innumerable memories. Given that ecologically valid event memories can easily surpass the level of complexity found in the AB-BC paradigm, it is important to consider how the process of memory integration can be limited to avoid creating infinitesimally large event memories. In the next section, we discuss how neural oscillations may provide a resolution to these issues.

## 3 | A ROLE FOR NEURAL OSCILLATIONS

Rhythmic fluctuations in neural activity are referred to as neural oscillations. Numerous empirical studies have demonstrated that the

synchronization of theta (3–7 Hz) and gamma (30–100 Hz) oscillations within the hippocampus relate to successful episodic memory formation (for review, see Colgin, 2015; Hanslmayr, Staerens, & Bowman, 2016; Nyhus & Curran, 2010). An increase in the synchronization of hippocampal gamma oscillations is thought to facilitate spike-timing-dependent plasticity (STDP; Axmacher, Mormann, Fernández, Elger, & Fell, 2006; Nyhus & Curran, 2010)—a form of long-term potentiation (LTP) that depends on the highly precise firing of presynaptic and postsynaptic neurons. Probing rat hippocampal neurons *in vitro*, Bi and Poo (1998) showed that the postsynaptic neuron must fire 20 ms (that is, 1 cycle of a gamma oscillation) after the presynaptic neuron to induce LTP. Given that these hippocampal neurons have been shown to lock gamma-band activity (Jutras, Fries, & Buffalo, 2009) and hippocampal gamma-band activity is predictive of memory formation (e.g., Griffiths et al., 2019; Long & Kahana, 2015), one could speculate that increases in the amplitude of hippocampal gamma oscillations reflect increases in STDP.

In regards to theta activity, the phase of the oscillation has been thought to dictate whether LTP or long-term depression (LTD) occurs (Huerta & Lisman, 1995; Hyman, Wyble, Goyal, Rossi, & Hasselmo, 2003; Pavlides, Greenstein, Grudman, & Winson, 1988). This has led to the suggestion that the peak of the theta cycle is optimal for memory encoding while the trough of the cycle is optimal for memory retrieval (Hasselmo, 2005). Indeed, computational models implementing this principle demonstrate how the hippocampus can effectively encode new temporal sequences and retrieve existing sequences without incurring catastrophic interference between the two processes (Shapiro, Turk-Browne, Botvinick, & Norman, 2017). Here, pattern separation would arise at the peak of the theta cycle to help bind discretized elements of the event through LTP, while pattern completion would occur during the theta trough allowing LTD to prevent any binding of the retrieved trace with current sensory input. Evidence that supports the idea of such a mechanism in humans is, however, incomplete. Nevertheless, pieces of the puzzle have been revealed. For example, Clouter, Shapiro, and Hanslmayr (2017) demonstrated that two stimuli presented at the same phase of theta are more likely to be successfully encoded than two stimuli that are presented at opposing phases, indicating that associative memory formation varies as a function of theta phase. Moreover, Kerrén, Linde-Domingo, Hanslmayr, and Wimber (2018) demonstrated that neural evidence for retrieved stimuli fluctuate at approximately 7 Hz, suggesting that episodic memory retrieval is also dependent on theta phase.

While the origins and proposed functions of hippocampal theta and gamma rhythms are distinct, gamma oscillations are frequently seen to nest within the ongoing theta cycle (Colgin & Moser, 2010)—a phenomenon known as theta-gamma phase-amplitude coupling. Numerous studies have demonstrated that theta-gamma coupling correlates with successful memory formation (Heusser, Poeppel, Ezzyat, & Davachi, 2016; Staudigl & Hanslmayr, 2013; Tort, Komorowski, Manns, Kopell, & Eichenbaum, 2009). Phase-amplitude coupling is thought to provide a neural code capable of recording sequences (Lisman & Jensen, 2013). Under this framework, each gamma cycle is thought to reflect the firing of a cell population that codes for a

unique element in the sequence. While the cell assemblies firing within a single gamma cycle are unlikely to represent highly detailed information about the sequence, they may act as an index that can “ping” the associated information-rich neocortical representation (Teyler & Rudy, 2007). For example, these gamma cycles would not code for every contour, color, and sound of a fire truck, but rather could point to the detailed neocortical representations of such information. The ongoing theta oscillation is thought to organize these gamma cycles into a sequence. Testing this idea, Bahramsharif, Jensen, Jacobs, and Lisman (2018) asked participants to retain a sequence of three letters for several seconds and examined whether gamma-band representations of these letters peaked at distinct phases of the theta cycle. Indeed, they found that gamma-band representations of the first letter peaked earlier in the theta cycle than the second letter, and representations of the second letter peaked earlier in the theta cycle than the third letter. This result demonstrates that theta-gamma phase-amplitude coupling can provide a neural framework that codes for sequences of stimuli. Heusser et al. (2016) expanded this finding to episodic memory by asking participants to encode a sequence of images and then testing their knowledge of the sequence. Theta-phase locked gamma power increased with the addition of each item to a sequence, and critically, the phase which gamma power locked to became progressively later for each successive item, indicating that every item was added to the end of the existing theta-gamma code. Importantly, it would appear that theta-gamma coupling not only provides a method to link together elements of an event, but also provides a method to maintain these elements for the duration of the event (Axmacher et al., 2010). Notably however, such a sequence cannot carry on indefinitely. Lisman and Idart (1995) demonstrated that the number of elements that can be stored within an event is limited by the number of gamma cycles that can fit on within the theta cycle, ensuring that no event can become overly complex (potentially resolving some of the unanswered questions relating to pattern separation/completion raised in the previous section). Indeed, it would seem that hippocampal theta-gamma phase-amplitude coupling can organize and maintain an abstract and manageable neural code capable of encoding sequences as episodic memories.

The proposed neural code supported by hippocampal theta-gamma coupling may appear vastly different to the proposed roles of hippocampal theta and gamma in isolation. However, the principles can be reconciled. Gamma oscillations within a theta-gamma code ensure that cell populations coding for each element fire approximately 20 ms after the preceding cell population fires for the preceding element. As discussed above, this temporally precise firing allows STDP to strengthen the synaptic connections between two cell populations and, in the case of a theta-gamma code, would create a chain of elements (first to second element, second to third element etc.). In other words, the ability for gamma oscillations to facilitate STDP makes it ideal for creating temporally sequenced memories. Theta-dependent plasticity, in turn, prevents this change of elements turning into a never-ending sequence. As gamma rides the peak of the theta cycle, a sequence can be generated through gamma-linked STDP (Bi & Poo, 1998) and further enhanced by theta-related LTP

(Huerta & Lisman, 1995; Pavlides et al., 1988). During the trough of the theta cycle however, gamma-related increases in STDP could become negated by theta-related LTD, terminating any associative change generated by gamma oscillations. A recent computational model implementing this concept has demonstrated that the combination of theta and gamma-related LTP is an effective method to form associative memories (Parish, Hanslmayr, & Bowman, 2018). One can push this idea further by suggesting that the replay of this sequence occurs at the trough of the theta cycle. Indeed, if the replay of an event occurs during the trough of the theta cycle (Hasselmo, Bodelón, & Wyble, 2002), any synaptic plasticity induced by gamma-related STDP would be negated by the theta-related LTD, ensuring that the retrieved memory is not bound to incoming sensory information unrelated to the memory. In sum, hippocampal theta-gamma coupling may not only be the most effective method for maintaining sequences (Lisman & Jensen, 2013), but also for encoding and retrieving these sequences.

#### 4 | THE CASE FOR EVENT CONJUNCTION

So far, we have discussed how (a) event segmentation dictates the formation of episodic memories, (b) these memories can be integrated across event boundaries, and (c) hippocampal theta-gamma coupling may provide a mechanism to maintain and encode episodic memories. Here, we entwine these threads to provide a new view on how episodic memories are formed through the process of event segmentation.

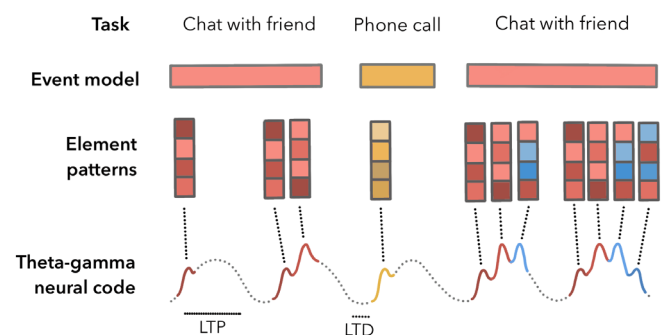
Take the following example: you are in a café with an old friend who is telling you a story about their new boss. You are interrupted by an urgent phone call so you step outside to answer, introducing a change in location and in goal. You then return to your friend, who resumes their story. This example includes two event boundaries, marked by leaving to answer the call and then returning to the café interior. Existing theories of event segmentation would predict that three distinct memories would be formed: (a) the details of the story told prior to the phone call, (b) the details of the phone call, and (c) the details of the story told after the phone call. Intuitively however, you are likely to recall the friend's story in its entirety despite the event boundaries that occurred between the telling of the story. In other words, integration has arisen to conjoin the two related events into a singular coherent memory. Indeed, we may further intuit that this integration would occur as the third event unfolds, because details from the first event (i.e., the beginning of the story) are essential to comprehending the details of the remaining story. We refer to the idea that two overlapping events can be integrated into a singular memory as *event conjunction*.\*

We propose that theta-gamma phase-amplitude coupling within hippocampus lies at the heart of event conjunction (see Figure 1). During the course of the first event, each element of the ongoing event is coded for by a unique hippocampal cell population locked to a discrete phase of the ongoing theta cycle (Bahramisharif et al., 2018; Lisman & Jensen, 2013). This event model is maintained within the hippocampus as a theta-gamma code for the duration of the event (Axmacher et al.,

2010). As the event unfolds and becomes more complex, new cell populations coding for new elements of the event are added to the end of the existing theta-gamma code (Heusser et al., 2016). The propensity for hippocampal theta-gamma coupling to induce LTP ensures that the ongoing event is steadily and proactively encoded as it unfolds. When an event boundary is encountered, the theta-gamma code is rapidly replayed during the peak of the theta cycle to facilitate additional retroactive encoding of the finalized event representation (Baldassano et al., 2017; Ben-Yakov & Henson, 2018; Sols et al., 2017). When another event boundary is encountered containing a cue to the previously encoded event, pattern completion leads to the reactivation of the earlier event through interactions between the hippocampus and medial prefrontal cortex (Backus et al., 2016; Schlichting & Preston, 2015). This reactivation would arise during the trough of the theta cycle (where LTD occurs) to ensure the reactivated trace is not bound to incoming sensory information, nor confounded by any encoding-related replay occurring during the same period (Colgin, 2015; Hasselmo et al., 2002; Schapiro et al., 2017). Detailed information about the original event is reinstated in the neocortex and then circled back to the hippocampus, where the theta-gamma code is recreated (Koster et al., 2018). Elements of the ongoing event are then appended to the recreated theta-gamma code in the same way in which new elements were added to the code during the unfolding of the original event. As a result, the current event becomes conjoined with the original event.

Five key predictions can be derived from this framework, each of which is discussed below:

1. *Events have an optimal duration.* Every theta cycle sees a repetition of the event's theta-gamma code, and hence every repetition sees



**FIGURE 1** The event conjunction framework. Event boundaries (e.g., answering a phone call) segment a continuous stream of experience into discrete events. These discrete events are represented within the brain as event models. Event models consist of a combination of “elements” (e.g., time, space, goals). As the event unfolds, more elements are added to the model. We propose that theta-gamma coupling within the hippocampus supports these event models by maintaining the temporal sequence of these elements and steadily encoding the event model during periods of long-term potentiation (LTP). At an event boundary, the current event model is replaced by a new model. The same happens to the theta-gamma code. When a boundary contains a cue to a previous event, that event is rapidly reactivated and subsequently updated with new elements relating to the new event [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



further strengthening of the event representation through LTP. Longer events, therefore, undergo more LTP than shorter events and hence will be better encoded. This is by no means a controversial prediction, as numerous studies have demonstrated that additional rehearsal time sees a boost in memory performance (e.g., Craik, 1970; Greene, 1987; Meunier, Ritz, & Meunier, 1972). Importantly however, overly long events may also be difficult to encode as they contain too many unique elements and hence cannot be maintained by a hippocampal theta-gamma code. As such, our framework would predict that there is an optimal duration for events; overly short events suffer too little LTP to be encoded, while overly long events become too complex to be encoded. While this idea has already been discussed in relation to associative memory (Lisman & Idart, 1995), our framework would also predict that this phenomenon generalizes to memory integration. Notably, this prediction would distinguish event conjunction from the processes of pattern completion/pattern separation, which would not predict a finite limit in the duration of an event. The optimal duration of an event, though, remains a mystery.

2. *The contents of the original event are more likely to be recalled than the second event.* Our framework proposes that the original event memory is reactivated and then cycled back to the hippocampus to recreate the theta-gamma code with information about the ongoing event conjoined to it. This means that two traces of the original event are available for retrieval (i.e., the original trace and the conjoined trace), whereas only a single trace of the second event is available (i.e., the conjoined trace). If the conjoined trace were to become distorted or lost, details of the original event may still be recalled from the original trace whereas details of the second event would be lost. As such, memory for the original event should be stronger than that for the second event. In support of this prediction, AB-BC integration paradigms show that memory performance for the first pair is greater than the second pair (Backus et al., 2016; Schlichting et al., 2014). Whether this difference applies to naturalistic events remains an open question however.
3. *The number of gamma cycles nested in the hippocampal theta oscillation should increase over the course of an event.* As an event unfolds, more details arise. The cell assemblies that code for these new details therefore need to be appended to the theta-gamma code that represents the event. Any additional event information requires additional gamma cycles to become nested in the theta oscillation. Heusser et al. (2016) have demonstrated such a phenomenon in sequence memory; the addition of an item to an existing sequence produces a shift in metrics of theta-gamma coupling. Our framework would predict that this effect arises regardless of whether the event is later remembered, as the maintenance of the theta-gamma code is essential to comprehending the ongoing event.
4. *The original theta-gamma code should be detectable during the unfolding of the second event.* Our framework posits that the original event is rapidly reactivated (Michelmann, Staresina, Bowman, & Hanslmayr, 2019; Pacheco Estefan et al., 2019; Yaffe, Shaikhouni, Arai, Inati, & Zaghoul, 2017) and reconstructed within the hippocampus when a related event begins. Therefore, we speculate that

the original theta-gamma code should be detected during the second event. Indeed, previous work has demonstrated that the unique aspect of one pair (i.e., A of pair AB) is reactivated when the individual is cued with the second pair (i.e., pair BC; Zeithamova et al., 2012). While this paradigm focused on time windows after the pairs AB and BC had been associated, we would postulate that the unique aspect of pair AB is also present during the learning of BC, demonstrating that the original event is reactivated during the second event.

5. *Event conjunction cannot occur after memory consolidation.* Consolidation sees the shift of episodic memories from a temporary store in the hippocampus to a more stable store in the neocortex (McClelland, McNaughton, & O'Reilly, 1995). Once a memory has been consolidated, we predict that it cannot be conjoined with an ongoing event in the manner described above as the original event memory is no longer accessible in the hippocampus. In line with this idea, Tse et al. (2007) demonstrated that the hippocampus was essential to the integration of two memories when sleep had not occurred between the two events (i.e., before consolidation). When the rodents had been allowed to sleep however, the hippocampus was no longer required for memory integration—perhaps because consolidation has reduced the dependence of integration on the hippocampus. We speculate that the same happens with event conjunction (to read more about how events are integrated with semantic knowledge and schemas, see Clewett et al., 2019).

## 5 | OPEN QUESTIONS

The section above has described the event conjunction framework, and elaborated on various predictions that can test its validity. However, several open questions remain. Here, we take a speculative look at possible resolutions to such questions.

Throughout this paper, we have loosely defined an “element” of an event as a discrete aspect of the event (e.g., a person, a location), but we have not focused heavily on how these elements are defined. Speculatively, we can envisage at least two ways in which these elements may be defined. First, the hierarchical network that detects event boundaries described by Baldassano et al. (2017) may discretize both events and elements. To recap, Baldassano et al. (2017) demonstrated that fine-grained aspects of the event are segregated by early sensory regions and abstract changes are segregated by more high-order regions including the posterior medial cortex. Perhaps it is these low-level boundaries that distinguish one element from another (i.e., a person from a location) while higher-order boundaries distinguish one event from another. Alternatively, hippocampal pattern separation may provide a means to disentangle overlapping elements of an event from one another. For example, if you were to enter a new restaurant and be greeted by an overenthusiastic *maitre-d'*, these two simultaneously presented elements (i.e., the person and the location) would need pattern separation to disentangle the elements prior to encoding. It will be interesting to see how these two processes contribute and/or interact to help define individual elements of an event.

So far, we have implicitly assumed that every event is of more-or-less equal length, but could there be a hierarchy of events? For example, could an event model of a film be made up of a series of event models for individual scenes? There is growing evidence to suggest that hippocampal representations of space shift along the longitudinal axis (Poppenk, Evensmoen, Moscovitch, & Nadel, 2013; Strange, Witter, Lein, & Moser, 2014). In humans, the most posterior portion of the hippocampus represents local space while the most anterior portion represents the more general environment (Brunec et al., 2018). If we apply these principles to event models, we would anticipate that the more focal event models are housed in the posterior hippocampus while more overarching models are housed in the anterior hippocampus (Collin, Milivojevic, & Doeller, 2015). This would provide multiple levels of event model, and quite possibly explain how event models for both extended events (i.e., a film) and short events (i.e., a scene within a film) can be encoded within the hippocampus.

Another interesting question revolves around the criteria required for the hippocampus to conjoin events or segment them. While conclusive answers are yet to be forthcoming, we speculate that the decision to conjoin/segment events hinges upon at least two criteria. First, we would anticipate that event conjunction is more likely to occur when the events share a large proportion of overlapping elements. When more elements overlap between events, there are inherently more cues to trigger the reinstatement of the original event. Second, we would anticipate that the overlapping elements of the two events must be salient aspects of both events. For example, if the location where both events occur is unimportant, then perhaps the spatial cue of that location is insufficient to spark conjunction. Together, one may speculate that for event conjunction to take place, there needs to be significant overlap between salient elements of the two events. What exactly constitutes threshold for “significant” or “salient” overlap remains an open question. It is also worth noting that these two criteria are not seen as an exhaustive list; other criteria may be yet identified.

Lastly, one may wonder how the concept of event models relates to ideas about the so-called “cognitive map.” A cognitive map serves to organize and relate experience to influence behavior across all cognitive domains (Tolman, 1948). On a neural level, the hippocampus has been thought to underpin these maps (O’Keefe & Nadel, 1978) as it creates relational links across space (Schiller et al., 2015), time (Schapiro, Kustner, & Turk-Browne, 2012) and social networks (Tavares et al., 2015). Intriguingly, substantial changes in environment can induce global remapping within the hippocampus (Wills, Lever, Cacucci, Burgess, & O’Keefe, 2005), whereby hippocampal neurons that represent one spatial map are “remapped” to represent another. If these principles generalize to cognitive maps (Ekstrom & Ranganath, 2018), then it would seem that the remapping of cognitive maps shares a remarkably high degree of conceptual similarity with how event boundaries segment event models (Brunec, Moscovitch, & Barense, 2018). Taking this idea further, one could speculate that event models require global remapping to maximally separate (i.e., orthogonalize) the hippocampal representation of two temporally adjacent yet unrelated events, and hence avoid interference from previous event models. During later

event conjunction, the original mapping would be reinstated (akin to the reinstatement of spatial maps when a rat revisits a previously explored environment; Wills et al., 2005), allowing the event model to be updated with new information using the original mapping scheme. Perhaps then, given the conceptual overlap between these two fields, it is possible that researchers of event cognition may benefit from studying the world of cognitive maps, while researchers of cognitive maps may benefit from getting to grips with event cognition.

## 6 | CONCLUSION

Episodic memories are carved out of continuous experience through event segmentation. Traditional theories of event segmentation view every event, and therefore every memory, as unique. This, however, contradicts our behavioral and electrophysiological understanding of human episodic memory. Here, we have proposed the “event conjunction framework.” We propose that two unique events which share a commonality can be integrated online (i.e., as the second event unfolds). On an electrophysiological level, we envisage this phenomenon depending on theta-gamma coupling within the hippocampus: elements of an event are represented within individual gamma cycles, with the phase of the theta cycle dictating the start and end of an event. During event conjunction, the theta-gamma code that represents a previously encoded event is reconstructed within the hippocampus and new details from the currently unfolding event are appended to the code. While some of the central tenets of this framework still require direct empirical investigation, our reinterpretation of existing results provides reassuring support for the framework.

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## ENDNOTE

\*Notably, the example above relates to the conjunction of two events which are separated by a single unrelated event. We predict, however, that additional events could be conjoined to these two if they also share central details (e.g., you step away for a second urgent phone call and return to the story for a third time, leading to conjunction between the first two sections of the story and the currently-unfolding third section). Similarly, event conjunction is not restricted by the number of unrelated events separating the two to-be-conjoined events. For example, you step away for the urgent phone call, head to the counter to order another coffee, then return to the story—here two boundaries segregate the parts of the story, but we would still anticipate conjunction.

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