

**ScienceDirect** 



# The ebb and flow of experience determines the temporal structure of memory David Clewett and Lila Davachi



Everyday life consists of a continuous stream of information, yet somehow we remember the past as distinct episodic events. Prominent models posit that event segmentation is driven by erroneous predictions about how current experiences are unfolding. Yet this perspective fails to explain how memories become integrated or separated in the absence of prior knowledge. Here, we propose that contextual stability dictates the temporal organization of events in episodic memory. To support this view, we summarize new findings showing that neural measures of event organization index how ongoing changes in external contextual cues and internal representations of time influence different forms of episodic memory.

### Address

Department of Psychology, New York University, USA

Corresponding author: Davachi, Lila (lila.davachi@nyu.edu)

Current Opinion in Behavioral Sciences 2017, 17:186-193

This review comes from a themed issue on  $\ensuremath{\textbf{Memory in time and space}}$ 

Edited by Lila Davachi and Neil Burgess

For a complete overview see the <u>Issue</u> and the <u>Editorial</u>

Available online 3rd October 2017

http://dx.doi.org/10.1016/j.cobeha.2017.08.013

2352-1546/© 2017 Elsevier Ltd. All rights reserved.

### Introduction

"Time is a sort of river of passing events, and strong is its current; no sooner is a thing brought to sight than it is swept by and another takes its place, and this too will be swept away." -Marcus Aurelius (c. 161–180 AD)

For millennia, the notion that moment-to-moment experiences unfold like a flowing river has been central to our conceptualizations of time. Yet while we experience the world through a constant stream of information, we usually remember those experiences as being more discrete and discontinuous, broken down into individual episodes, or memories. This raises two fundamental yet often unasked questions: *What makes an episode in episodic memory? How do we represent time and extract information about events embedded within it?*  Prior memory research has largely focused on examining the processes that contribute to successful encoding of individual trial information, such as single images or single item-context associations. In the real world, however, more complex modes of memory clustering are necessary to derive meaning from past experiences. Growing evidence indicates that such memory organization has reliable consequences not only for later event recall and recognition of individual items [1–4] but also for how the temporal, or sequential, aspects of events are remembered [5\*\*,6,7,8\*,9,64]. Thus, discerning the cognitive and neural processes by which we organize, structure, and remember events is essential to promoting a deeper understanding of how our memory systems contribute to adaptive behavior.

Prominent models of event cognition posit that ongoing sensory inputs are segmented into events when our expectations about the current environment conflict with what is happening, leading to prediction errors [10,11]. From this perspective, prior knowledge enables inferences to be made about the structure of specific sequences of information, or events [12]. For instance, participants tend to agree on natural breakpoints in videos of familiar everyday activities, such as washing a car [10]. However, this prediction error account of event segmentation is incomplete (Box 1). While prior experience may call to mind and reinforce the temporal structure of familiar events, we cannot rely fully on predictions garnered from past experiences to parse novel sequences of information. Further, recent empirical work shows that foreshadowing impending event shifts during reading comprehension still leads to slower reading times, suggesting that expectations do not prevent event segmentation processes from occurring [13]. Most segmentation and memory studies have also focused overwhelmingly on recognition memory [4,14–17]. In so doing, they obscure the simple fact that episodic memories are primarily characterized by their rich sequential and contextual information [18].

In this short review, we argue that fluctuations in contextual stability — including changes in stimulus features, goal states, or internal representations of time — fundamentally shape the temporal organization of events in episodic memory. To support this view, we summarize evidence that even the simplest transitions between contexts during sequence learning modulate behavioral and neural encoding/retrieval processes in ways that can both form and distinguish unique episodic events across time.

### Box 1 Prediction . . . Error? Re-thinking the role of prediction in event memory.

Influential models of event perception posit that segmentation is driven by a mismatch between the current event model, or working memory representation of what is happening, and actual sensory inputs [10,11]. However, this account has not been substantiated with empirical data, with interpretations being drawn from reverse inference [56]. Furthermore, event segmentation has been shown repeatedly to occur without explicit prediction errors. For instance, there is evidence that event structure can emerge from predictive temporal clustering in the absence of surprise or prediction errors [23\*\*]. As described in the main text, event structure emerges simply through context changes during novel episodic encoding and therefore do not require expectations about how new experiences will unfold overtime [6]. Moreover, there are indications that event-model updating still occurs even when event shifts in a text narrative are not surprising [13]. While more research on this topic is needed, we favor the view that prediction errors may be one among many cognitive or perceptual processes (e.g. memory updating, conflict, task switching etc.) that determine event clustering based on moment-to-moment changes in external or internal contextual states [57,58].

### Encoding new memories of distinct sequential events

If one accepts the premise that individual episodic events contain sequential representations that are strongly integrated while, at the same time, separated and distinguishable from adjacent events, one can then ask how this structure emerges. Theoretically, unified sequential events could emerge from a continuous influx of information through the integration of sequential representations with a shared context, the separation of items that span a change in context, or both. Recent inquiry along these lines has led to a wealth of new behavioral and brain data suggesting that contextual stability and change contribute to the extraction of discrete episodic events from ongoing experience.

In the first empirical test of these hypotheses, Ezzyat and Davachi used narrative stimuli that described a protagonist completing an everyday activity [19<sup>••</sup>]. Even though the activities were familiar to participants, the transitions, or boundaries, between adjacent sentences were manipulated by inserting a simple three-word phrase that conveyed a short or long passage of time: either 'a moment later' or 'A while later'. This simple phrase had significant consequences on later memory. Namely, participants were significantly less likely to recall information across an event boundary than they were to recall successive sentences within an event. Critically, this was the case even though the absolute time that passed during reading was the same.

Consistent with evidence from the event comprehension literature [20–22], these findings provided important behavioral evidence that discrete episodic memories emerge from our interpretation of the pauses, breaks, and changes in event context. In this same study, FMRI was used to determine whether neural measures of within-event integration and/or across-event separation determined individual differences in memory binding across time. We found that memory integration performance was associated with gradual increases in medial temporal lobe (MTL) cortex, ventral striatum, and medial PFC activation across the course of an event. On the other hand, event separation, or reduced memory binding across events, was associated with reduced univariate activation in lateral PFC and middle temporal gyrus at boundaries.

# Neural mechanisms supporting within-event memory integration

In the moment of experiencing something new, what information does the brain use to guide sequential integration? Preserving sequential order information appears to rely on binding sequential items to a shared context, such as similar perceptual/conceptual features or task set [6]. Supporting this idea, temporal memory has now repeatedly been shown to be better for information experienced within a context compared to information experienced across contexts [5\*\*,7,8\*,9,19\*\*], even though the absolute amount of time passed is the same (Figure 1b).<sup>1</sup>

Neuroimaging data have linked these mnemonic effects to greater similarity in hippocampal activation patterns across time [5\*\*]. For instance, DuBrow and Davachi had participants learn a list of images grouped into event sequences separated by a category change (e.g. faces or objects; Figure 1a). After encoding, temporal memory was tested. An index of contextual stability was formulated by considering the amount of representational change across time. We found that encoding stability in hippocampal multivariate patterns between the two tested items was related to temporal memory accuracy, with more stable encoding patterns predicting better recency memory. Critically, hippocampal pattern stability was a significantly better predictor of temporal memory than the univariate hippocampal activation during study of each item. This finding suggests that the temporal stability of hippocampal representations helps determine whether sequential links are preserved in memory. Although beyond the scope of this paper, there is also evidence that neural oscillations play an important role in integrating sequential representations within events (Box 2).

Extending the findings from Ezzyat and Davachi, recent studies suggest that the medial prefrontal cortex (mPFC)

<sup>&</sup>lt;sup>1</sup> This temporal binding effect is seen for relatively short sequences of information. On the other hand, there are indications that people may rely more on item memory strength rather than associative information to make accurate recency discriminations for two items from longer sequences (see [21] for Discussion).





Encoding-related and retrieval-related patterns of hippocampal activity relate to the preservation of sequential memory representations across time. (a) Participants viewed a stream of celebrity faces or objects in which there were intermittent category switches, or event boundaries. Having participants form a meaningful narrative between items encouraged temporal order encoding. Later, participants performed a recency discrimination test between two items from the same category that either spanned a boundary ('Switch') or did not ('No Switch'). (b) Recency memory for item pairs with an intervening boundary was impaired relative to item pairs that did not contain an intervening boundary. (c) A pattern classifier was used to quantify evidence of intervening item reactivation (i.e. the three encoding items that had been shown between the two recency test items) during memory retrieval. (Left panel) If faces evidence simply reflected the *perceptual features* of the probe items, there would be equal face evidence across the two trial types from encoding. However, if intervening items were reactivated from memory during retrieval, the prediction would be that face evidence would be greater for 'no switch' trials than 'switch trials' despite the perceptual inputs (faces) being the same (right panel). (d) Supporting the latter prediction, the classifier identified significantly more evidence of intervening item patterns of activity during retrieval for no-switch (e.g. 3 faces) versus switch trials (e.g. 2 objects and one face), despite the category of images (e.g. faces) being the same for both conditions during retrieval. \*p < .05.

may act independently and/or in concert with the hippocampus to facilitate temporal memory binding of contextually related elements. For instance, mPFC is engaged throughout the duration of a learned context [23<sup>••</sup>]. At the functional network level, accurate versus inaccurate serial recall for within-context sequential information corresponds with enhanced vmPFC-hippocampal functional connectivity at encoding [7]. Overall, these findings dovetail with the idea that dynamic interactions between the mPFC and hippocampus support temporal order memory [24,25] as well as the integration of sensory inputs into bound, associative memories more generally [26].

### Box 2 Theta-gamma phase coding as a mode of integration [64].

Another critical question is how the brain preserves memory for sequential order *within* a specific event. Based on examination of place cell firing in the hippocampus of rodents running in a maze, it has long been theorized that a sequence of items can be represented along distinct phases of theta oscillations [59,60]. Recent human work using MEG has provided evidence for theta-gamma phase coding during encoding of six-item sequence [61]. Specifically, it was found that gamma power during each item peaked at a distinct and consecutive phase of an underlying theta oscillation. Furthermore, this structured phase coding relates to successful temporal order memory for those sequences. However, several issues remain unresolved. For example, it is unclear whether theta phase oscillations reset at event boundaries and whether this relates to sequential memory impairments observed across these boundaries.

# Maintaining contextual representations preserves ongoing memory integration

Thus far, we have reviewed evidence that contextual change reduces the sequential binding of representations. Yet there are instances where we can bridge these transitions in memory. Neuroimaging data suggest that enhanced temporal stability in hippocampal representations preserves across-event sequential memory binding [5<sup>••</sup>,27]. Furthermore, current data suggest that linking memories across boundaries can be facilitated by encouraging active retrieval of prior representations during encoding [5<sup>••</sup>,28]. Supporting this view, implicit memory tests reveal that sequential representations are linked together irrespective of boundaries when implementing an associative encoding strategy [5<sup>••</sup>].

Memory integration processes therefore are not only influenced by attending to sensory changes in the environment but rather are also modulated by an individual's goal state (e.g. [9]). Current FMRI data indicate that hippocampal retrieval mechanisms may contribute to this form of active integration. For example, increased hippocampal activity at event transitions correlates with successful serial recall across those transitions [7]. The fact that this pattern did not relate to within-event recall argues that hippocampal activation at event boundaries may reflect retrieval processes targeted to reactivate the just-encountered pre-boundary information. In turn, this memory reactivation may facilitate memory binding across the boundary. Consistent with this idea, prior work suggests that the reactivation of just-encoded information is associated with increased hippocampal activation [16,62].

Studies using naturalistic movies have also revealed a post-stimulus hippocampal 'offset' signal that predicts gist memory for a just-seen movie clip [29–31] and neural event reactivation in supramarginal gyrus during free recall [32<sup>•</sup>]. While these studies did not explicitly test across-event integration, a recent scalp EEG study showed that boundary-triggered rapid replay of just-

encoded events predicts participant's later sequential recall across those boundaries [63]. This finding suggests, beyond simply enhancing within-event binding for just-encoded information, boundary-triggered neural replay can also bridge boundaries in memory, at least under certain conditions (e.g. when using an associative encoding strategy).

Past work also shows that activation in lateral prefrontal cortex (PFC) is important for encoding of temporal order information across event boundaries [7,19<sup>••</sup>]. Like the hippocampus, lateral PFC has been implicated in representing temporal contextual information [23<sup>••</sup>,25,33], and facilitating relational memory binding across small gaps in time [34–38]. Lesion evidence also shows that the lateral PFC contributes to temporal order memory under conditions when top-down attentional control is required [39]. Taken together, these data support the notion that boundaries can be bridged in memory using strategic retrieval, as indexed by both hippocampal and lateral PFC activation at boundaries.

# Evidence for 'unitization' of episodes in memory

There are multiple brain mechanisms that might support better recall of within-event sequences compared to across-event sequences. One possibility is that a retrieval cue may lead to the reinstatement of the event context (e.g. temporal information) that then, in turn, facilitates access to other event information. In fact, there is strong evidence that context reinstatement during retrieval facilitates the recall of neighboring items [40]. While not mutually exclusive, another possibility is that once an episodic sequence is formed, the sequential links between items may have been strengthened such that when shown one item, the sequence itself is reinstated or replayed.

To test these hypotheses explicitly, DuBrow and Davachi trained a classifier to distinguish between faces and objects. This classifier was then applied to memory retrieval trials where participants were shown two probe stimuli from the same category and asked to report which item appeared more recently. Critically the two probe stimuli during encoding were always separated by three intervening items during encoding, and were either from the same 'event' or spanned an event boundary (Figure 1c). The classifier output revealed a higher level of face evidence for a face retrieval trial that was from a 'face event' during encoding compared to a face retrieval trial that contained intervening objects (Figure 1d). Importantly, the difference in classifier output could not be driven by perceptual information, as these trial types during retrieval were perceptually identical.

These results strongly suggest that the intervening study items are reinstated during temporal recency judgments. However, one could argue that the classifier was also sensitive to the reinstatement of a more general face 'context' associated with each event. To more directly address this, a behavioral experiment was performed that was nearly identical to the original study, except participants performed an old/new memory judgment on single items from the study list after each recency discrimination. Critically, those test items were either intervening items from the sequence or were preceding items (i.e. within the same category). We found that 'old' recognition decisions were made significantly faster for intervening items compared to a preceding item from the same visual category [5<sup>••</sup>], providing behavioral evidence for the reinstatement of intervening items from a sequence during temporal memory judgments. Interestingly, this finding aligns with recent evidence that lateral PFC and hippocampal pattern stability carries positional code information during encoding that is also reinstated at retrieval [41].

# Event reinstatement during repeated encoding

Unlike novel, or episodic, sequential encoding, we can use prior knowledge to orchestrate sequential memory integration for familiar events. This topic has been reviewed elsewhere [6], but briefly, it has been shown that as distinct sequence information becomes more familiar with learning, a temporal prediction signal is evident such that hippocampal activation patterns become more temporally correlated with repetition [42,43]. One function of this hippocampal forward prediction, or pattern completion, mechanism may be to preserve stable contextual signals that promote sequential integration in memory. Indeed, human fMRI studies have shown that multivoxel hippocampal activation patterns become more dissimilar between separate welllearned sequences/pairs compared to within well-learned sequences/pairs, suggesting that individual sequences become more distinct after learning [43–45]. Importantly, these data support the idea that there is sequential 'unitization' of discrete event memories during repeated learning. Moreover, this hippocampal mechanism may be similar to pattern completion processes that are engaged during intervening item reactivation at retrieval (e.g. **[5**<sup>••</sup>]).

### Temporal drift as a mode of event separation

People tend to have better memory for information that appears close together in time [46]. According to temporal context models, mnemonic clustering effects arise from successive stimuli becoming associated through a slowly evolving temporal context signal [47]. In this way, temporally adjacent items become integrated through their transient contextual overlap, whereas items appearing farther apart in time are more likely to become separate memories due to less contextual overlap. Supporting this model, electrophysiological recordings in rodent have But what happens to this contextual signal at event boundaries? An extension of these models proposes that a sudden disruption or shift in active contextual representations isolates different sets of list items [49]. In turn, separated items tend to cluster more closely together in free recall, invoking the integration and separation of contextually distinct events. Building on this work, recent computational modeling evidence shows that speeding up a time-varying contextual signal at event boundaries can account for behavioral findings of impaired temporal memory across context transitions [8<sup>•</sup>].

Fluctuations in the rate of temporal signal drift may also relate to observations that event boundaries lead to exaggerated estimates of event sequence duration [50]. For instance, items appearing within the same scene context were remembered as 'closer' together than items spanning a scene change [27], even though the same amount of objective time had passed. Like sequential integration [5<sup>••</sup>], these apparent time distortions in memory were linked to greater hippocampal pattern stability during encoding, with more stability relating to judgments of closer temporal proximity [27]. More recent neuroimaging evidence showed that retrospective judgments of time duration were associated with reduced entorhinal cortex pattern similarity between two clips during encoding [51].

Given that neural pattern stability predicts both time compression and within-event memory integration, these studies suggest an intimate relationship between mnemonic representations of time and memory organization of distinct events. The nature of this relationship, however, is somewhat unclear. On the one hand, by propelling temporal signals further adrift, contextual shifts may benefit temporal order memory by linking stimuli to more distinct temporal contextual representations in the hippocampus [48], lateral prefrontal cortex [52], and/or medial prefrontal cortex [53]. On the other hand, by dilating temporal representations to create the illusion of greater event separation, rapid temporal signal changes at event boundaries may lead to impaired temporal memory binding, as other empirical [5<sup>••</sup>,7,8<sup>•</sup>,9] and theoretical [49] work suggest.

### **Open questions**

Although the studies reviewed here have advanced our understanding of how episodic memories emerge from continuous experience, several important questions remain. First, studies in the event cognition literature use a diverse range of stimuli, including text narratives, video clips, and item sequences to probe perception and memory of event structure. Moreover, the way event boundaries are defined differs from study-to-study, leaving open whether the effects of perceptual or task switches on sequence memory differ from the effects of transitioning from one daily activity to another. From the perspective that shared context is critical for event extraction, we'd still expect any form of contextual change to influence different aspects of episodic memory in a similar manner. Even so, additional work is needed to reconcile potentially disparate findings concerning the mechanisms that mediate the impact of context on episodic memory organization.

Second, in the real world, event comprehension does not necessarily rely on preserving the precise order of sequential representations, which in many cases may be fragile. Instead, people's recall of past experiences is usually strong for sequences of information containing causal structure [54]. Interestingly, recent work also shows participants rarely detect mis-ordered portions of videos of daily activities [55], reinforcing the idea that prediction errors may not be necessary for perceiving or comprehending event structure. Addressing these issues will provide a deeper understanding of episodic memories help us derive meaning from everyday experiences.

### Conclusion

A growing number of studies suggest that moment-tomoment changes in context dynamically modulate the separation and integration of sequential representations to form discrete episodic memories. Exciting new research implicates the hippocampus and PFC as the

### Figure 2



Schematic diagram highlighting core mechanisms by which contextual stability and transitions determine the temporal structure of episodic memories. (a) During an experience, the continuous influx of sensory inputs and our internal thoughts are integrated into coherent events according to their shared context. Likewise, discrete episodes are distinguished and separated from temporally adjacent information by shifts in context [5\*\*,6,7,8\*,9,19\*\*,64]. (b) Hypothesized model of information accumulation across stable contexts. When contextual inputs suddenly change, such as moving from a park to a city street, the active event representation is dropped and information accumulation begins for the new context. These contextual shifts serve as 'event boundaries' that impair memory integration yet, in so doing, facilitate memory separation in time. This hypothesized effect of shared context on within-event memory integration is distinguished from Event Segmentation Theory [10], which focuses on prediction errors leading to enhanced encoding of boundary information. (c) The stability of activity patterns in the hippocampus indexes contextual stability and the integration of information across time [5\*\*,42]. Increased communication between the hippocampus and BFC (not shown) supports within-event integration during familiar or novel experiences [7]. On the other hand, when one's goal is to preserve sequential links in memory, active retrieval processes in the hippocampus and lateral PFC trigger the reinstatement of pre-boundary information [7,19\*\*]. (d) When we recall past experiences, they retain their temporal structure and remain separated as distinct episodic events [5\*\*]. However, even when the passage of time was the same, we subjectively remember information spanning context changes as occurring farther apart time, whereas within-event information is remembered as occurring closer together [27].

critical brain regions supporting these processes, with potentially dissociable roles for PFC sub-regions: whereas temporal stability in hippocampal activation patterns and connectivity with medial PFC appear to promote withineven integration, hippocampal and lateral PFC activation at boundaries appears to promote linking memories across discrete events (Figure 2). Together these findings suggest that neural measures of event organization are a powerful tool for understanding how fluctuations in external and internal contextual states during an experience modulate mnemonic integration and separation processes across time.

### **Conflict of interest statement**

Nothing declared.

### **Acknowledgements**

This project was funded by federal NIH Grant R01 MH074692 to L.D. and by a fellowship on federal NIH Grant T32 MH019524 to D.C.

### References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- •• of outstanding interest
- 1. Flores S, Bailey H, Eisenberg M, Zacks J: Event segmentation improves event memory up to one month later. J Exp Psychol Learn Mem Cogn 2017.
- Pettijohn KA, Thompson AN, Tamplin AK, Krawietz SA, Radvansky GA: Event boundaries and memory improvement. *Cognition* 2016, 148:136-144.
- Sargent JQ, Zacks JM, Hambrick DZ, Zacks RT, Kurby CA, Bailey HR, Eisenberg ML, Beck TM: Event segmentation ability uniquely predicts event memory. Cognition 2013, 129:241-255.
- 4. Swallow KM, Zacks JM, Abrams RA: Event boundaries in perception affect memory encoding and updating. *J Exp Psychol Gen* 2009, **138**:236.
- 5. DuBrow S, Davachi L: Temporal memory is shaped by encoding
- stability and intervening item reactivation. J Neurosci 2014, 34:13998-14005.

This study showed that context changes impair temporal order memory. Using a combination of multivoxel pattern stability and pattern classification, this study also showed that encoding-related and retrieval-related patterns of hippocampal activity predict sequential memory integration — and its preservation — across time.

- 6. Davachi L, DuBrow S: How the hippocampus preserves order: the role of prediction and context. *Trends Cogn Sci* 2015, **19**:92-99.
- 7. DuBrow S, Davachi L: Temporal binding within and across events. Neurobiol Learn Mem 2016, 134:107-114.
- Horner AJ, Bisby JA, Wang A, Bogus K, Burgess N: The role of spatial boundaries in shaping long-term event representations. *Cognition* 2016, 154:151-164.

This study showed that crossing through a doorway impairs temporal order memory, much in the same manner as visual contextual changes. Using a computational model, they demonstrated that increasing the rate of a drift of a temporal contextual signal could account for these behavioral impairments.

- DuBrow S, Davachi L: The influence of context boundaries on memory for the sequential order of events. J Exp Psychol Gen 2013, 142:1277.
- Zacks JM, Speer NK, Swallow KM, Braver TS, Reynolds JR: Event perception: a mind-brain perspective. Psychol Bull 2007, 133:273.

- Reynolds JR, Zacks JM, Braver TS: A computational model of event segmentation from perceptual prediction. *Cogn Sci* 2007, 31:613-643.
- 12. Bower GH, Morrow DG: Mental models in narrative comprehension. *Science* 1990, 247:44-49.
- Pettijohn KA, Radvansky GA: Narrative event boundaries, reading times, and expectation. Mem Cognit 2016, 44:1064-1075.
- 14. Radvansky GA, Tamplin AK, Krawietz SA: Walking through doorways causes forgetting: Environmental integration. *Psychon Bull Rev* 2010, **17**:900-904.
- 15. Radvansky GA, Copeland DE: Walking through doorways causes forgetting: situation models and experienced space. *Mem Cognit* 2006, **34**:1150-1156.
- Swallow KM, Barch DM, Head D, Maley CJ, Holder D, Zacks JM: Changes in events alter how people remember recent information. J Cogn Neurosci 2011, 23:1052-1064.
- 17. Newtson D, Engquist G: The perceptual organization of ongoing behavior. J Exp Soc Psychol 1976, 12:436-450.
- Tulving E: Episodic memory: from mind to brain. Annu Rev Psychol 2002, 53:1-25.
- Ezzyat Y, Davachi L: What constitutes an episode in episodic
  memory? Psychol Sci 2011, 22:243-252.

This study showed that brain regions (MTL, ventral striatum, mPFC) that were sensitive to narrative event structure also promoted memory integration within-events. In addition, other brain regions (lateral PFC, MTG) were impacted by event boundaries, or transitions, in ways that affected across-event memory binding.

- 20. Zwaan RA: Processing narrative time shifts. J Exp Psychol Learn Mem Cogn 1996, 22:1196.
- 21. Rinck M, Weber U: Who when where: an experimental test of the event-indexing model. *Mem Cognit* 2003, **31**:1284-1292.
- 22. Speer NK, Zacks JM: Temporal changes as event boundaries: processing and memory consequences of narrative time shifts. *J Mem Lang* 2005, **53**:125-140.
- 23. Schapiro AC, Rogers TT, Cordova NI, Turk-Browne NB,
- Botvinick MM: Neural representations of events arise from temporal community structure. Nat Neurosci 2013, 16:486-492.
   This study showed that 'natural breakpoints' can be identified based on temporal clustering or a shared temporal context, between subsets of

temporal clustering, or a shared temporal context, between subsets of information. Importantly, these segmentation effects were observed in the absence of any prediction errors or surprise, suggesting there are other mechanisms that may be involved in discretizing events.

- Barker GR, Banks PJ, Scott H, Ralph GS, Mitrophanous KA, Wong L-F, Bashir ZI, Uney JB, Warburton EC: Separate elements of episodic memory subserved by distinct hippocampalprefrontal connections. Nat Neurosci 2017.
- 25. Ranganath C, Hsieh LT: The hippocampus: a special place for time. Ann NY Acad Sci 2016, 1369:93-110.
- Preston AR, Eichenbaum H: Interplay of hippocampus and prefrontal cortex in memory. Curr Biol 2013, 23:R764-R773.
- Ezzyat Y, Davachi L: Similarity breeds proximity: pattern similarity within and across contexts is related to later mnemonic judgments of temporal proximity. *Neuron* 2014, 81:1179-1189.
- 28. DuBrow S, Davachi L: Commentary: Distinct neural mechanisms for remembering when an event occurred. Front Psychol 2017, 8.
- Ben-Yakov A, Dudai Y: Constructing realistic engrams: poststimulus activity of hippocampus and dorsal striatum predicts subsequent episodic memory. J Neurosci 2011, 31:9032-9042.
- Ben-Yakov A, Eshel N, Dudai Y: Hippocampal immediate poststimulus activity in the encoding of consecutive naturalistic episodes. J Exp Psychol Gen 2013, 142:1255.
- 31. Ben-Yakov A, Rubinson M, Dudai Y: Shifting gears in hippocampus: temporal dissociation between familiarity and

novelty signatures in a single event. *J Neurosci* 2014, **34**:12973-12981.

- 32. Baldassano C, Chen J, Zadbood A, Pillow JW, Hasson U,
- Norman KA: Discovering event structure in continuous narrative perception and memory. *bioRxiv* 2016:081018.
   This study showed that dynamic videos can be segmented into discrete

events based on the stability/similarity of brain activity patterns across time. This study also identified a hippocampal event-offset signal that predicted reactivation of neural patterns representing those events during free recall.

- Polyn SM, Kahana MJ: Memory search and the neural representation of context. Trends Cogn Sci 2008, 12:24-30.
- Blumenfeld RS, Ranganath C: Dorsolateral prefrontal cortex promotes long-term memory formation through its role in working memory organization. J Neurosci 2006, 26:916-925.
- Blumenfeld RS, Ranganath C: Prefrontal cortex and long-term memory encoding: an integrative review of findings from neuropsychology and neuroimaging. *Neuroscientist* 2007, 13:280-291.
- Hales JB, Brewer JB: The timing of associative memory formation: frontal lobe and anterior medial temporal lobe activity at associative binding predicts memory. J Neurophysiol 2011, 105:1454-1463.
- Hales JB, Israel SL, Swann NC, Brewer JB: Dissociation of frontal and medial temporal lobe activity in maintenance and binding of sequentially presented paired associates. *J Cogn Neurosci* 2009, 21:1244-1254.
- Qin S, Piekema C, Petersson KM, Han B, Luo J, Fernández G: Probing the transformation of discontinuous associations into episodic memory: an event-related fMRI study. Neuroimage 2007, 38:212-222.
- Mangels JA: Strategic processing and memory for temporal order in patients with frontal lobe lesions. *Neuropsychology* 1997, 11:207-221.
- Manning JR, Polyn SM, Baltuch GH, Litt B, Kahana MJ: Oscillatory patterns in temporal lobe reveal context reinstatement during memory search. Proc Natl Acad Sci 2011, 108:12893-12897.
- Kalm K, Norris D: A shared representation of order between encoding and recognition in visual short-term memory. *Neuroimage* 2017, 155:138-146.
- Paz R, Gelbard-Sagiv H, Mukamel R, Harel M, Malach R, Fried I: A neural substrate in the human hippocampus for linking successive events. Proc Natl Acad Sci 2010, 107:6046-6051.
- Schapiro AC, Kustner LV, Turk-Browne NB: Shaping of object representations in the human medial temporal lobe based on temporal regularities. *Curr Biol* 2012, 22:1622-1627.
- Hsieh L-T, Gruber MJ, Jenkins LJ, Ranganath C: Hippocampal activity patterns carry information about objects in temporal context. Neuron 2014, 81:1165-1178.
- Kalm K, Davis MH, Norris D: Individual sequence representations in the medial temporal lobe. J Cogn Neurosci 2013, 25:1111-1121.
- Kahana MJ: Associative retrieval processes in free recall. Mem Cognit 1996, 24:103-109.

- Howard MW, Kahana MJ: A distributed representation of temporal context. J Math Psychol 2002, 46:269-299.
- Manns JR, Howard MW, Eichenbaum H: Gradual changes in hippocampal activity support remembering the order of events. *Neuron* 2007, 56:530-540.
- Polyn SM, Norman KA, Kahana MJ: A context maintenance and retrieval model of organizational processes in free recall. *Psychol Rev* 2009, 116:129.
- 50. Faber M, Gennari SP: In search of lost time: reconstructing the unfolding of events from memory. *Cognition* 2015, 143:193-202.
- Lositsky O, Chen J, Toker D, Honey CJ, Shvartsman M, Poppenk JL, Hasson U, Norman KA: Neural pattern change during encoding of a narrative predicts retrospective duration estimates. *eLife* 2016, 5:e16070.
- Jenkins LJ, Ranganath C: Prefrontal and medial temporal lobe activity at encoding predicts temporal context memory. J Neurosci 2010, 30:15558-15565.
- Jenkins LJ, Ranganath C: Distinct neural mechanisms for remembering when an event occurred. *Hippocampus* 2016.
- Brownstein AL, Read SJ: Situation models and memory: the effects of temporal and causal information on recall sequence. *Memory* 2007, 15:730-745.
- Hymel A, Levin DT, Baker LJ: Default processing of event sequences. J Exp Psychol Hum Percept Perform 2016, 42:235.
- Zacks JM, Kurby CA, Eisenberg ML, Haroutunian N: Prediction error associated with the perceptual segmentation of naturalistic events. J Cogn Neurosci 2011, 23:4057-4066.
- Zwaan RA, Langston MC, Graesser AC: The construction of situation models in narrative comprehension: an eventindexing model. *Psychol Sci* 1995, 6:292-297.
- Radvansky GA: Across the event horizon. Curr Dir Psychol Sci 2012, 21:269-272.
- Lisman JE, Idiart MA: Storage of 7 plus/minus 2 short-term memories in oscillatory subcycles. Science 1995, 267:1512.
- Jensen O, Lisman JE: Hippocampal CA3 region predicts memory sequences: accounting for the phase precession of place cells. *Learn Mem* 1996, 3:279-287.
- Heusser AC, Poeppel D, Ezzyat Y, Davachi L: Episodic sequence memory is supported by a theta-gamma phase code. Nat Neurosci 2016.
- Öztekin I, McElree B, Staresina BP, Davachi L: Working memory retrieval: contributions of the left prefrontal cortex, the left posterior parietal cortex, and the hippocampus. J Cogn Neurosci 2009, 21:581-593.
- Sols I, DuBrow S, Davachi L, Feuntemilla L: Event boundaries trigger rapid memory reinstatement of the prior event to promote their representation in long-term memory. *Curr Biol* (in press).
- 64. Heusser A, Ezzyat Y, Shiff I, Davachi L: Perceptual boundaries cause mnemonic trade-offs between local boundary processing and across-trial associative binding. *J Exp Psychol Learn Mem Cogn.* (in press).