

Retrieved-context models of memory search and the neural representation of time

Sean M Polyn and Rebecca A Cutler



Episodic memories are defined as taking place in a particular spatiotemporal context, that is, in a particular time and place. How the neural system constructs a representation of time is an open question. The perceptual characteristics of stimuli can be manipulated, allowing one to characterize corresponding changes in neural signal, but time is invisible, and cannot be manipulated directly. However, we can look at the structure and operation of computational models of memory to determine the predicted properties of a neural representation of temporal context. These predictions have been examined in a number of recent studies, reviewed here.

Address

Department of Psychology, Vanderbilt University, Nashville, TN 37240, United States

Corresponding author: Polyn, Sean M (sean.polyn@vanderbilt.edu)

Current Opinion in Behavioral Sciences 2017, **17**:203–210

This review comes from a themed issue on **Memory in time and space**

Edited by **Lila Davachi** and **Neil Burgess**

<http://dx.doi.org/10.1016/j.cobeha.2017.09.007>

2352-1546/© 2017 Published by Elsevier Ltd.

Time and episodic memory

Life is a continually unfolding succession of events. As one moves through the world, the details of these events are tied to the time and place of their occurrence, sometimes in a rough way, and sometimes with great specificity. The cognitive system responsible for associating the details of a particular experience to a particular spatiotemporal context is known as episodic memory [1*,2]. The episodic memory system involves both associative and executive processes, and supports the retrieval of details of past experience, allowing one to review their past, and imagine their future [3]. In laboratory-based memory tasks, time is an important determinant of behavioral performance. Recently studied materials have a strong advantage on memory tests [4], and memory for the order of events can be long-lasting [5]. The effect of time on performance is not always straightforward. In some cases, forgetting occurs quite rapidly as time passes

[6,7], and in other cases, seemingly forgotten associations can recover with the passage of time [8].

No one has yet developed a grand unified theory of the myriad effects of time on memory. Large gaps exist in our understanding of how the cognitive system represents time, and how a temporal representation might be used by the cognitive system to organize and retrieve one's experience. However, theorists have been working steadily on this problem for the past several decades, yielding a variety of formal models that describe potential structures and processes engaged to solve the problem of the cognitive representation of time. A common feature to many of these models is the idea that a temporal representation should change gradually as time passes, such that events that happened nearby in time have similar temporal representations associated with them [9,10**,11,12**,13]. These temporal representations serve as context to one's ongoing experience, in that they form a background that can be associated with the details of particular events, defining the episode of episodic memory. If these associations are bidirectional, then this gives the memory system a great deal of power: The details of a particular event can be used to retrieve the temporal context it occurred in, and the details of a particular temporal context can be used to retrieve the events that occurred while it prevailed [12**].

In this review, we will focus on retrieved-context models of memory search, which describe how the cognitive system could use integrative neural processes to construct a representation of temporal context, and how this context representation could be used to search through the contents of memory. These models were originally designed to explain behavioral performance in the free-recall task, which provides a simplified version of life's continually unfolding succession of events. In this task, participants study a series of verbalizable items, and are then prompted to recall them in whatever order they come to mind. One can learn a great deal about the structure of memory by examining the particular order in which memories are retrieved in free recall [14]. Time is a dominant organizational factor, as demonstrated by the contiguity effect: After recalling a particular item, the next item tends to come from a nearby list position [15,16]. Retrieved-context models provide a set of simple cognitive mechanisms that can explain a wide variety of behavioral phenomena in memory search tasks. They also provide a framework for interpreting the functional significance of neural signals recorded during these tasks,

allowing us to generate testable hypotheses regarding how behavioral phenomena and neural signals arise from a set of well-specified cognitive operations.

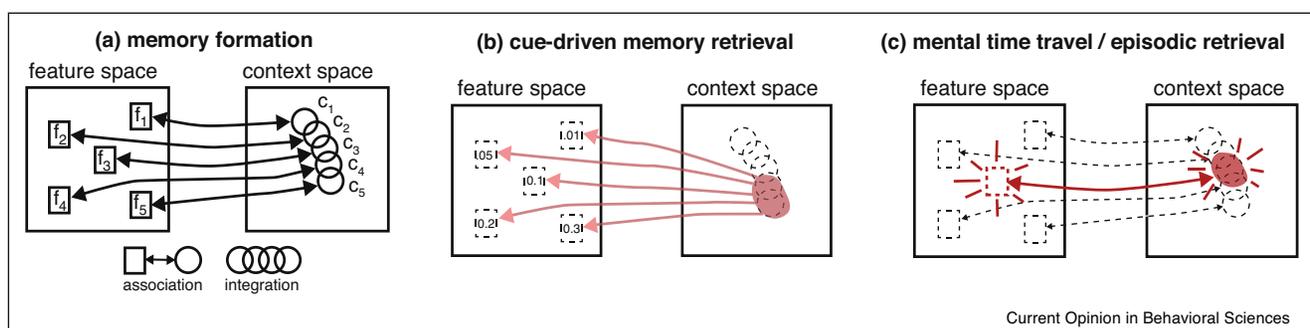
Retrieved-context models of episodic memory

The first published retrieved-context model, the Temporal Context Model (TCM; [12^{**}]), was designed to account for the recency and contiguity effects of free recall. TCM is implemented as a simplified neural network model with two layers of neurons (depicted schematically in Figure 1). One set of neurons represents the features of studied items (the feature layer), but generally could be thought to hold higher-order perceptual information regarding the perceptual environment of the participant, which could include the identity of studied words, the visual characteristics of pictures or objects, and the surrounding spatial environment. The second set of neurons (the context layer) uses integrative machinery to construct a temporal context representation. Items are assumed to have been seen or considered many times before, in many different contexts, and pre-existing synaptic connections link each item representation to a corresponding pre-experimental context representation. As such, when an item is studied, these item-to-context associations allow the system to retrieve contextual information associated with past experiences the person has had with the item. Integrative machinery in the context layer blends this retrieved pre-experimental context with whatever activity pattern is currently being maintained in the context layer. This integrative blending causes the temporal context representation to change gradually as new information is processed by the system. As such, the state of the context layer is sensitive to the recent history of the model's experience, as contextual information associated with past items fades gradually as new items are encountered.

Episodic memory is dependent on reciprocal associative connections projecting from the feature layer to context layer, and from the context layer to feature layer. These associations are rapidly modified during the study period to bind each studied item to the prevailing state of temporal context. During memory search, these episodic associations allow the system to use the temporal context representation as a retrieval cue, prompting the system to retrieve item representations associated with a particular state of context. The gradual change of the context representation over time provides temporal structure to memory, in that experiences that happened nearby in time will be linked to similar states of context. Polyn *et al.* [17] likened the dynamics of the contextual retrieval cue to a spotlight sweeping across the contents of memory, as depicted in Figure 2. In terms of the model, the contextual retrieval cue activates a blend of item representations, and there is a competition to determine which item representation becomes fully activated. Once an item representation is reactivated, two things happen: The item is reported, and the item-to-context associative connections are used to retrieve contextual states associated with the item. The newly formed episodic associations allow the system to retrieve the contextual state that was active at the moment the item was studied. This recovered context makes the memories from around that moment more accessible; this allows the model to account for temporal organization in recall response sequences, and could be a general purpose mechanism to support reminiscence.

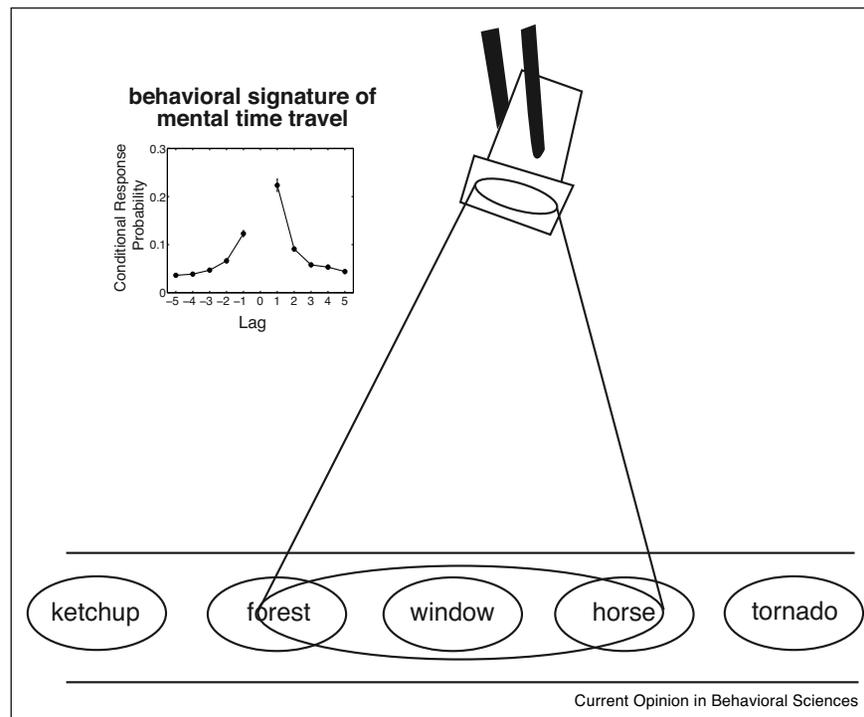
Over the past 15 years, this framework has been extended and modified to account for a wide variety of behavioral phenomena. TCM-A [18] included a set of accumulators to simulate response latency and account for the effect of distraction on performance. The Context Maintenance and Retrieval model (CMR) [17] added mechanisms to

Figure 1



Schematic overview of the core cognitive mechanisms of retrieved-context models of memory. **(a)** Memory formation. Associative processes forge links between representations of studied items and a gradually changing representation of context during the study period. **(b)** Cue-driven memory retrieval. During memory search, the contextual representation is projected through episodic associative structures to reactivate representations of the studied material. The strength of support for each item is indicated numerically. **(c)** Mental time travel/episodic retrieval. A reactivated item can prompt the system to retrieve the context state originally associated with that item during the study period.

Figure 2



The spotlight analogy. The contextual retrieval cue can be thought of as a spotlight, with the studied items placed at even intervals across a stage. During memory search the spotlight shines on the contents of memory, with the context-to-item associative connections determining which items the spotlight shines on. After an item is recalled, retrieved context centers the spotlight on the part of the stage where the remembered item was placed during study. The shifted spotlight illuminates items from neighboring serial positions of the just-recalled item, giving those neighbors an advantage in the ensuing recall competition. This mechanism supports temporal organization in free recall, where neighboring items on the study list tend to be reported successively. (Inset) A lag-based conditional response probability (lag-CRP) analysis reveals temporal organization in free recall. After recalling a particular item, the next recalled item tends to come from a nearby position on the study list.

account for organizational effects related to the source and semantic identity of the studied items. Howard and colleagues showed that this integrative contextual mechanism could also be used to construct spatial representations [19] and semantic representations [20]. The model has been applied to consolidation effects [21], the spacing effect [22], proactive interference and recall errors [23], differences in performance across groups and individuals [24,25], and the nature of episodic and semantic interactions during memory search [26].

A gradually changing temporal context representation provides continuity to an experience by causing temporally proximal events to cohere with one another in memory. As such, a disruption of this temporal representation could be used to partition experience. If the representational state of context changes dramatically, events that occur post-disruption will not be linked to events that occurred pre-disruption. Studies examining this have disrupted memory with task shifts [17,27], category shifts [28], words in a narrative indicating the passage of time [29], and having participants pass through a spatial boundary like a doorway [30]. Context-based

models can simulate these disruptions as an increased probability of a representational shift in the context representation [17,31]. In a retrieved-context model, a transient increase in the rate of integration would cause the context representation to leap forward [17]. Returning to the spotlight analogy, it would create a large gap between two items successively placed on the stage. With such a disruption, the spotlight could shine on the item on one side of the gap, and hardly illuminate the items on the far side. This could be a mechanism for creating distinct episodes in episodic memory, and perhaps more generally for creating event boundaries during ongoing experience [32,33].

Neural studies of temporal representations

The cognitive operations of retrieved-context models provide a good starting point for developing a neuroscientific theory of how a representation of time might be constructed and used by the brain [34,35]. A number of recent studies have used multivariate pattern analysis (MVPA; [36]) and representational similarity analysis (RSA; [37]) to find evidence of neural signals with dynamics consistent with a temporal representation. In these

studies, neural activity across a set of voxels (in fMRI) or across a set of electrodes (in scalp EEG and ECoG) is sampled at various time points in an experiment. Each time point provides a multivariate neural activity pattern. If studied items are drawn from categories known to elicit distinct patterns of brain activity, MVPA can be used to track the strength of category-specific neural signals both as the material is learned, and during a memory test [38]. The retrieved-context models described above were developed to explain how the dynamics of item and context representations relate to behavioral performance. Here, we review a number of studies that have used these model representations to interpret the functional significance of dynamic neural signals recorded as people perform memory tasks.

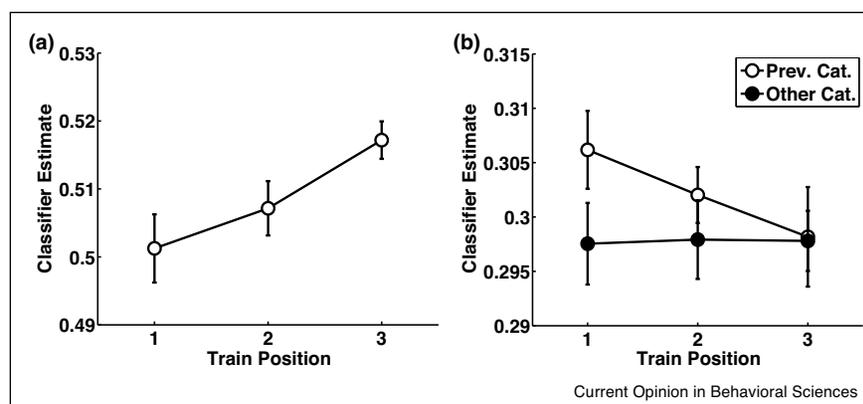
Morton *et al.* [39] recorded scalp EEG signal as participants studied lists of items drawn from three neurally discriminable categories (celebrities, landmarks, and objects). They constructed a multivariate neural activity pattern for each study item, where the features of each pattern were wavelet-based estimates of oscillatory power at several frequency bands (for every electrode) during the interval following stimulus onset. These distributed patterns of oscillatory activity contained information about the category of a studied item, and were also sensitive to the recent stimulus history, as shown in Figure 3. The rise and fall of these category-specific patterns was predictive of category clustering (recalling items from the same category successively) during a later free recall test. These neural dynamics are consistent with the operation of a temporal context representation. When a series of items from the same category are studied, each will likely retrieve a blend of item-specific and category-

specific contextual details. The integrative mechanism will blend these retrieved representations together, emphasizing the category-specific details common to the items, and improving a classifier's ability to identify the current category. This same blending operation will cause information related to the previous category to fade gradually. If this context representation is later used to probe memory, a strong category-specific signal at study should support organization of retrieved memories by category (as was observed). Morton and Polyn [40] replicated this finding of integrative category-related activity and showed that both the integrative neural signal, and the behavioral phenomenon of category clustering are disrupted by an inter-item distraction task (mental arithmetic).

Chan *et al.* [41] also found a relationship between integrative category activity and recall behavior in an fMRI study of free recall (using the same stimulus categories as above). They structured study lists such that items from a target category were preceded equally often by members of each of two other non-target categories. They found that there was variability in how strongly the preceding category information persisted during the study of the target item. Target items with a lot of residual activation from the same preceding non-target category tended to group together during a later recall period, even though the items came from distant parts of the study list. This is consistent with the idea that the residual non-target category information is integrated into a retrieval cue that is constructed as the study list progresses.

Medial temporal lobe (MTL) brain structures are known to play a critical role in episodic memory processes [42].

Figure 3



Category-related neural activity shows integrative dynamics. Morton *et al.* [39] used MVPA to track category information in scalp EEG signal as participants studied mixed lists of celebrities, landmarks, and objects (memory was tested using free recall). (a) As a train of same-category items is presented, the classifier's estimate of the current category increases, indicating that category-specific activity is integrated over multiple item presentations. (b) Activity related to the previous category declines with train position, again consistent with integration over multiple items. Activity related to the other category (not current or previous) serves as a baseline, and does not decline with train position of the current category.

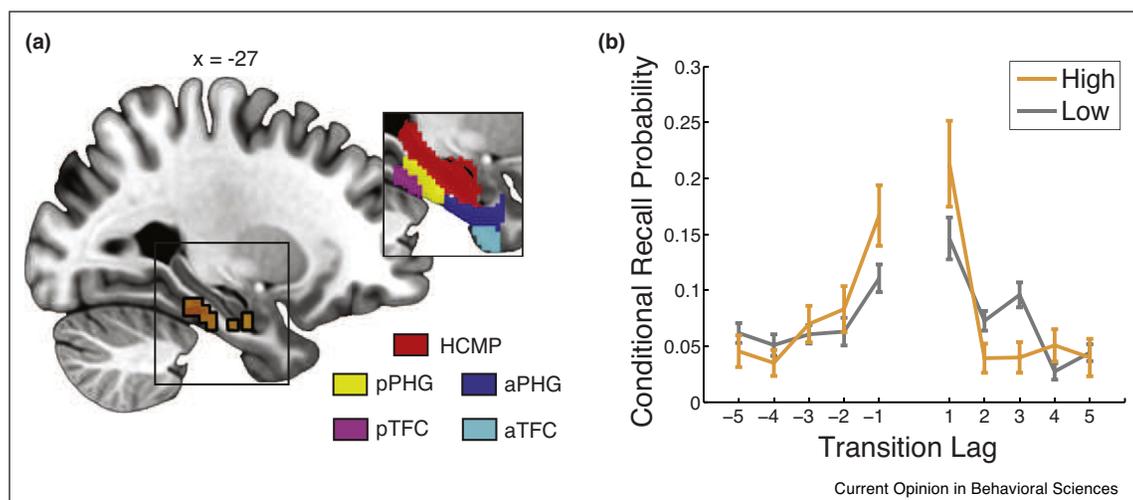
Data from Morton *et al.* [39] *Cerebral Cortex*.

A number of studies have examined the dynamics of neural activity patterns in MTL as a sequence of items are viewed, and have found that these patterns display context-like properties [43]. Many of these studies use RSA to calculate the pairwise similarities of neural activity patterns (usually using either a correlation-based or cosine measure) [37]. The level of similarity between two patterns has been used as a proxy for contextual evolution (when study-period patterns are being compared with one another), or as a proxy for contextual retrieval (when recall-period patterns are compared with study patterns). Hsieh *et al.* [44] used RSA to show that well-learned sequences of items elicit highly similar hippocampal activity patterns across repeated presentation of the sequence, and that these patterns are highly sensitive to temporal context. They found that the same item embedded in two different well-learned sequences elicited two distinct neural patterns, and that when an item was embedded in a randomly ordered sequences there wasn't clear evidence for either item or position information in the neural patterns. The dynamics of MTL activity patterns have also been related to behavioral performance on memory tests. Ezzyat and Davachi [45] found that items associated with similar neural patterns (from hippocampus) were later judged to come from nearby positions in a study list. Similarly, DuBrow and Davachi [46] found that increased hippocampal similarity between two items was predictive of successful performance on a later recency discrimination. In contrast, Jenkins and Ranganath [47] found that more dissimilar

hippocampal patterns at study were predictive of successful recency discrimination, and Jenkins and Ranganath [48] found an area of rostralateral PFC where dissimilarity between successive patterns at study predicted good performance on a temporal reconstruction task. More work is needed to determine whether pattern similarity or pattern dissimilarity during study is more conducive to good temporal memory; this work may benefit from computational simulation of temporal discrimination tasks [35] to determine whether different task variants may be differentially sensitive to pattern similarity (with some tasks benefitting from more similarity, and some benefitting from less).

Other studies have examined neural activity during the memory test itself, looking for neural activity with dynamics consistent with the operation of a contextual retrieval cue. Kragel *et al.* [49] found neural signal in posterior hippocampus and adjacent parahippocampal cortex that increased when successively recalled items came from nearby list positions, linking these regions to temporal organization and contextual processing, as shown in Figure 4. DuBrow and Davachi [46] found that MVPA category estimates taken during a recency discrimination reflected the category identity of the items intervening between the two probed items on the study list. This suggests that contextual information from the study period is being reactivated to support the recency discrimination. This is consistent with a study by Ritchey *et al.* [50] finding that recognition memory performance is

Figure 4



Linking fMRI BOLD activity to contextual retrieval. (a) Kragel *et al.* [49] used a neural-behavioral retrieved-context model to identify a cluster of voxels in medial temporal lobe that were informative for the context retrieval operation in the model. HCMP, hippocampus; aPHG and pPHG, anterior and posterior parahippocampal gyrus; aTFC and pTFC, anterior and posterior temporal fusiform cortex. (b) Neural responses were partitioned into high-activity (High) and low-activity (Low) recall events, where High responses were >0.5 SDs above the mean response. The behavioral recall events were partitioned according to whether the MTL response was High or Low. The graph characterizes temporal organization in the two sets of recall events. There is an enhanced likelihood of short-lag transitions for high-activity MTL events (i.e., when MTL activity is high, the next response is more likely to come from a nearby list position to the prior response). Data from Kragel *et al.* [49] *Journal of Neuroscience*.

enhanced when the neural activity pattern recorded during the test of a particular item matches the pattern recorded when the item was originally studied. Along similar lines, Manning *et al.* [51] found that the pattern of intracranial ECoG activity during recall of an item matched the pattern recorded when that item was studied, and showed graded similarity to patterns for neighboring study items, consistent with the retrieval of a gradually changing temporal representation. Howard *et al.* [52] found a similar effect in intracranial single-unit activity as participants viewed a sequence of stimuli in a continuous recognition paradigm. The overall pattern of single-unit activity changed gradually, and when an item was repeated, a component of the neural activity pattern matched the pattern observed just before the item's first presentation. Electrophysiological studies of neural activity in rodents have also found evidence of gradually changing neural activity patterns that relate to the animal's behavior [53,54].

Open questions

Many questions remain regarding the nature of the cognitive processes supporting memory search, and how these processes give rise to the wide variety of behavioral phenomena observed over more than a century of experimental work. Here, we focused our review on the representation of time, and its role as an organizational factor in memory. However, there are many other kinds of information that have powerful effects on memory organization, such as semantic knowledge [55] and source characteristics [56]. The studies by Morton and colleagues described above suggest that semantic information is integrated into a representation of temporal context. This aligns with behavioral studies demonstrating the complexity of temporal and semantic interactions in memory search, such as those examining how category clustering is affected by the spacing of items in the study list, and how category-related interference is affected by the timing of presentation of study materials [40,57–62]. The development of computational models to account for the interactions between episodic and semantic memory may allow us to bridge between our theories of how meaningful perceptual stimuli are coded neurally [63–71] and our theories of the neural representation of time.

Conclusions

Retrieved-context models describe a set of cognitive processes that work together to support memory search. These models have been successful in accounting for a wide variety of behavioral phenomena from the free-recall task and its variants. We believe these models provide a starting point for thinking about how the neural system might construct a representation of time, and how it might use such a representation to organize and probe memory. As such, these models may help us interpret the potential functional significance of temporally sensitive neural signals in memory tasks.

Conflict of interest statement

Nothing declared.

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. Tulving E: **Episodic and semantic memory**. In *Organization of Memory*. Edited by Tulving E, Donaldson W. New York: Academic Press; 1972:381–403.
- In which Tulving lays out detailed definitions for these now-canonical memory systems.
2. Tulving E: **Episodic memory: from mind to brain**. *Annu Rev Psychol* 2002, **53**:1–25 <http://dx.doi.org/10.1146/annurev.psych.53.100901.135114>.
3. Schacter DL, Addis DR, Buckner RL: **Episodic simulation of future events**. *Ann N Y Acad Sci* 2008, **1124**:39–60.
4. Murdock BB: **The serial position effect of free recall**. *J Exp Psychol* 1962, **64**:482–488.
5. Yntema DB, Trask FP: **Recall as a search process**. *J Verbal Learn Verbal Behav* 1963, **2**:65–74.
6. Ebbinghaus H: *On Memory: A Contribution to Experimental Psychology*. New York: Teachers College, Columbia University; 1885/1913.
7. Sperling G: **The information available in brief visual presentation**. *Psychol Monogr* 1960, **74**:22.
8. Briggs GE: **Acquisition, extinction, and recovery functions in retroactive inhibition**. *J Exp Psychol* 1954, **47**:285–293.
9. Estes WK: **Statistical theory of spontaneous recovery and regression**. *Psychol Rev* 1955, **62**:145–154.
10. Bower GH: **Stimulus-sampling theory of encoding variability**. In **•• Coding Processes in Human Memory**. Edited by Melton AW, Martin E. New York: John Wiley and Sons; 1972:85–121. (Chapter 5).
- In this classic paper, Bower describes a representational theory of memory, laying the groundwork for modern memory models.
11. Mensink G-JM, Raaijmakers JGW: **A model for interference and forgetting**. *Psychol Rev* 1988, **95**:434–455.
12. Howard MW, Kahana MJ: **A distributed representation of **•• temporal context****. *J Math Psychol* 2002, **46**:269–299.
- This paper provides a detailed exploration of the first retrieved-context model.
13. Brown GDA, Neath I, Chater N: **A temporal ratio model of memory**. *Psychol Rev* 2007, **114**:539–576.
14. Puff CR (Ed): *Memory Organization and Structure*. New York: Academic Press; 1979.
15. Kahana MJ: **Associative retrieval processes in free recall**. *Mem Cogn* 1996, **24**:103–109.
16. Kahana MJ, Howard MW, Polyn SM: **Associative retrieval processes in episodic memory**. In *Cognitive Psychology of Memory. Vol 2 of Learning and Memory: A Comprehensive Reference, 4 vols. (J. Byrne, Ed.)*. Edited by Roediger III HL. Oxford: Elsevier; 2008:467–490.
17. Polyn SM, Norman KA, Kahana MJ: **A context maintenance and retrieval model of organizational processes in free recall**. *Psychol Rev* 2009, **116**:129–156.
18. Sederberg PB, Howard MW, Kahana MJ: **A context-based theory of recency and contiguity in free recall**. *Psychol Rev* 2008, **115**:893–912.
19. Howard MW, Fotedar MS, Datey AV, Hasselmo ME: **The temporal context model in spatial navigation and relational learning: toward a common explanation of medial temporal lobe function across domains**. *Psychol Rev* 2005, **112**:75–116.

20. Howard MW, Shankar KH, Jagadisan UKK: **Constructing semantic representations from a gradually changing representation of temporal context.** *Top Cogn Sci* 2011, **3**:48-73.
21. Sederberg PB, Gershman SJ, Polyn SM, Norman KA: **Human memory consolidation can be explained using the temporal context model.** *Psychonom Bull Rev* 2011, **18**:455-468.
22. Lohnas LJ, Polyn SM, Kahana MJ: **Contextual variability in free recall.** *J Mem Lang* 2011, **64**:249-255.
23. Lohnas LJ, Polyn SM, Kahana MJ: **Expanding the scope of memory search: modeling intralist and interlist effects in free recall.** *Psychol Rev* 2015, **122**:337-363.
24. Howard MW, Kahana MJ, Wingfield A: **Aging and contextual binding: modeling recency and lag-recency effects with the temporal context model.** *Psychonom Bull Rev* 2006, **13**:439-445.
25. Healey MK, Kahana MJ: **Is memory search governed by universal principles or idiosyncratic strategies?** *J Exp Psychol Gen* 2014, **143**:575-596.
26. Morton NW, Polyn SM: **A predictive framework for evaluating models of semantic organization in free recall.** *J Mem Lang* 2016, **86**:119-140.
27. Polyn SM, Norman KA, Kahana MJ: **Task context and organization in free recall.** *Neuropsychologia* 2009, **47**:2158-2163.
28. DuBrow S, Davachi L: **The influence of context boundaries on memory for the sequential order of events.** *J Exp Psychol Gen* 2013, **142**:1277-1286.
29. Ezzyat Y, Davachi L: **What constitutes an episode in episodic memory?** *Psychol Sci* 2011, **22**:243-252.
30. Radvansky GA, Tamplin AK, Krawietz SA: **Walking through doorways causes forgetting: environmental integration.** *Psychonom Bull Rev* 2010, **17**:900-904.
31. 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.
32. Zacks JM, Tversky B: **Event structure in perception and conception.** *Psychol Bull* 2001, **127**:3.
33. Zacks JM, Speer NK, Swallow KM, Braver TS, Reynolds JR: **Event perception: a mind-brain perspective.** *Psychol Bull* 2007, **133**:273-293.
34. Polyn SM, Kahana MJ: **Memory search and the neural representation of context.** *Trends Cogn Sci* 2008, **12**:24-30.
35. Howard MW, Shankar KH, Aue WR, Criss AH: **A distributed representation of internal time.** *Psychol Rev* 2015, **122**:24.
36. Norman KA, Polyn SM, Detre GJ, Haxby JV: **Beyond mind-reading: multi-voxel pattern analysis of fMRI data.** *Trends Cogn Sci* 2006, **10**:424-430.
37. Kriegeskorte N, Mur M, Bandettini PA: **Representational similarity analysis — connecting the branches of systems neuroscience.** *Front Syst Neurosci* 2008, **2**:1-28.
38. Polyn SM, Natu VS, Cohen JD, Norman KA: **Category-specific cortical activity precedes retrieval during memory search.** *Science* 2005, **310**:1963-1966.
39. Morton NW, Kahana MJ, Rosenberg EA, Baltuch GH, Litt B, Sharan AD, Sperling MR, Polyn SM: **Category-specific neural oscillations predict recall organization during memory search.** *Cereb Cortex* 2013, **23**:2407-2422.
40. Morton NW, Polyn SM: **Beta-band activity represents the recent past during episodic encoding.** *Neuroimage* 2017, **147**:672-702.
41. Chan SCY, Applegate MC, Morton NW, Polyn SM, Norman KA: **Lingering representations of stimuli influence recall organization.** *Neuropsychologia* 2017, **97**:72-82.
42. Milner B, Squire LR, Kandel ER: **Cognitive neuroscience and the study of memory.** *Neuron* 1998, **20**:445-468.
43. Turk-Browne NB, Simon MG, Sederberg PB: **Scene representations in parahippocampal cortex depend on temporal context.** *J Neurosci* 2012, **32**:7202-7207 <http://dx.doi.org/10.1523/JNEUROSCI.0942-12.2012>.
44. Hsieh L-T, Gruber MJ, Jenkins LJ, Ranganath C: **Hippocampal activity patterns carry information about objects in temporal context.** *Neuron* 2014, **81**:1165-1178 <http://dx.doi.org/10.1016/j.neuron.2014.01.015>.
45. 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.
46. DuBrow S, Davachi L: **Temporal memory is shaped by encoding stability and intervening item reactivation.** *J Neurosci* 2014, **34**:13998-14005.
47. Jenkins LJ, Ranganath C: **Distinct neural mechanisms for remembering when an event occurred.** *Hippocampus* 2016, **26**:554-559.
48. Jenkins LJ, Ranganath C: **Prefrontal and medial temporal lobe activity at encoding predicts temporal context memory.** *J Neurosci* 2010, **30**:15558-15565.
49. Kragel JE, Morton NW, Polyn SM: **Neural activity in the medial temporal lobe reveals the fidelity of mental time travel.** *J Neurosci* 2015, **35**:2914-2926.
50. Ritchey M, Wing EA, LaBar KS, Cabeza R: **Neural similarity between encoding and retrieval is related to memory via hippocampal interactions.** *Cereb Cortex* 2013, **23**:2818-2828 <http://dx.doi.org/10.1093/cercor/bhs258>.
51. Manning JR, Polyn SM, Baltuch G, Litt B, Kahana MJ: **Oscillatory patterns in temporal lobe reveal context reinstatement during memory search.** *Proc Natl Acad Sci U S A* 2011, **108**:12893-12897.
52. Howard MW, Viskontas IV, Shankar KH, Fried I: **Ensembles of human MTL neurons “jump back in time” in response to a repeated stimulus.** *Hippocampus* 2012, **22**:1833-1847.
53. Manns JR, Howard MW, Eichenbaum H: **Gradual changes in hippocampal activity support remembering the order of events.** *Neuron* 2007, **56**:530-540 <http://dx.doi.org/10.1016/j.neuron.2007.08.017>.
54. Hyman JM, Ma L, Balaguer-Ballester E, Durstewitz D, Seamans JK: **Contextual encoding by ensembles of medial prefrontal cortex neurons.** *Proc Natl Acad Sci* 2012, **109**:5086-5091.
55. Bousfield WA: **The occurrence of clustering in the recall of randomly arranged associates.** *J Gen Psychol* 1953, **49**:229-240.
56. Johnson MK, Hashtroudi S, Lindsay DS: **Source monitoring.** *Psychol Bull* 1993, **114**:3-28.
57. Puff CR: **Clustering as a function of the sequential organization of stimulus word lists.** *J Verbal Learn Verbal Behav* 1966, **5**:503-506.
58. Glanzer M: **Distance between related words in free recall: trace of the STS.** *J Verbal Learn Verbal Behav* 1969, **8**:105-111.
59. Wickens DD: **Encoding categories of words: an empirical approach to meaning.** *Psychol Rev* 1970, **77**:1-15.
60. Gardiner JM, Craik FIM, Birtwistle J: **Retrieval cues and release from proactive inhibition.** *J Verbal Learn Verbal Behav* 1972, **11**:778-783.
61. Batchelder WH, Riefer DM: **Separation of storage and retrieval factors in free recall of clusterable pairs.** *Psychol Rev* 1980, **87**:375-397.
62. Polyn SM, Erlikhman G, Kahana MJ: **Semantic cuing and the scale-insensitivity of recency and contiguity.** *J Exp Psychol Learn Mem Cogn* 2011, **27**:766-775.
63. Hubel DH, Wiesel TN: **Receptive fields, binocular interaction and functional architecture in the cat's visual cortex.** *J Physiol* 1962, **160**:106.

64. Gross CG, Bender DB, Rocha-Miranda CE: **Visual receptive fields of neurons in inferotemporal cortex of the monkey.** *Science* 1969, **166**:13030-21306.
65. Logothetis NK, Pauls J, Poggio T: **Shape representation in the inferior temporal cortex of monkeys.** *Curr Biol* 1995, **5**:552-563.
66. Miller EK, Erickson CA, Desimone R: **Neural mechanisms of visual working memory in prefrontal cortex of the macaque.** *J Neurosci* 1996, **16**:5154.
67. Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P: **Distributed and overlapping representations of faces and objects in ventral temporal cortex.** *Science* 2001, **293**:2425-2429.
68. Kamitani Y, Tong F: **Decoding the visual and subjective contents of the human brain.** *Nat Neurosci* 2005, **8**:679-685.
69. Kriegeskorte N, Mur M, Ruff DA, Kiani R, Bodurka J, Esteky H, Tanaka K, Bandettini PA: **Matching categorical object representations in inferior temporal cortex of man and monkey.** *Neuron* 2008, **60**:1126-1141.
70. Huth Alexander G, Nishimoto Shinji, Vu An T, Gallant Jack L: **A continuous semantic space describes the representation of thousands of object and action categories across the human brain.** *Neuron* 2012, **76**:1210-1224.
71. Tong F, Pratte MS: **Decoding patterns of human brain activity.** *Annu Rev Psychol* 2012, **63**:483-509.