

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

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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.

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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.

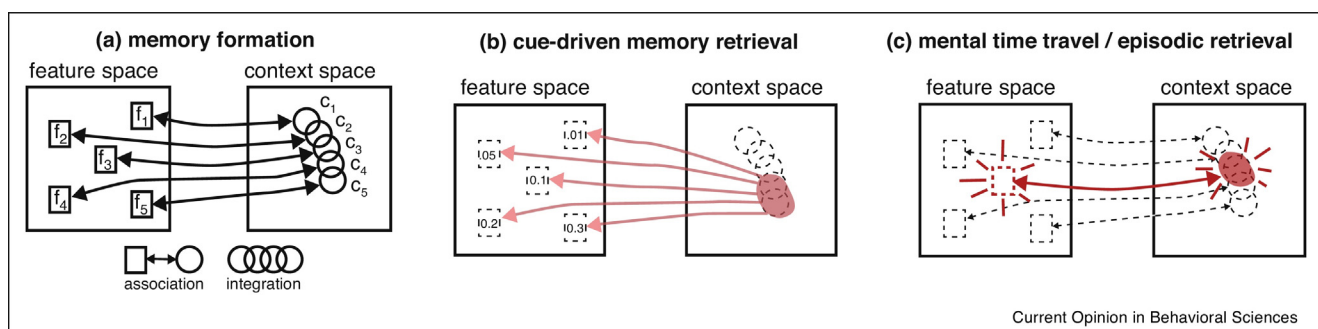
Retrieved-context models of episodic memory

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.

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