# Using Context to Search Memory: Functional Roles of the Medial Temporal Lobe and Prefrontal Cortex

*James Kragel*

The ability to search one's past for a specific memory amongst similar occurrences is a hallmark feature of the episodic memory system. Context-based theories of episodic memory retrieval propose that a slowly changing contextual representation allows for the construction of discrete, separable episodes. A review of recent neuroimaging, neuropsychological, and electrophysiological evidence suggests that activity within the medial temporal lobe (MTL) may support such a contextual representation, while control processes within the prefrontal cortex may influence the maintenance and updating of representations within the MTL.

**Keywords:** *Episodic memory, medial temporal lobe, prefrontal cortex*

**Episodic memory:** Memory of events, incorporating contextual information such as the time, place, and emotional state of the memory.

**Item recognition:** A memory task in which participants must determine whether a stimulus has been presented previously.

**Source memory:** Memory for contextual details associated with a particular episode.

## Introduction

Cognitive theories of episodic memory posit that memory retrieval involves patterns of neural activity returning to a previous state[1, 2], resulting in the subjective experience of 'mental time travel'[3]. These cognitive models rely on a contextual representation that integrates information over long time scales, representing information about both the environment and internal states. When an item is encoded into memory, associations are formed between the item representation and the current state of context. This associative link allows for two different processes to occur: 1) a state of context can be used to retrieve particular items from memory; and 2) particular items can be used to retrieve contextual information, such as the location or time in which they were studied. When an item is retrieved, the context in which it was studied may also be retrieved, causing the contextual representation to return to its prior state. A growing body of evidence supporting the representation of item information within posterior cortical regions, as well as their reactivation during memory retrieval, will be reviewed. While there is ample support for the neural representation of item-specific information, only recent investigations have begun to search for neural mechanisms that may mediate a contextual representation. Findings from the neuroimaging and neuropsychological literature that support the role of MTL and prefrontal regions in the processing of contextual information will be reviewed.

## Reactivation of cortical activity during retrieval

Recent neuroimaging studies provide evidence that retrieval of a previously bound episode occurs when the cortical activity present when the memory is constructed is reactivated. Studies examining cortical reactivation typically have similar experimental form, in which a particular cue is presented during the encoding of an episodic memory. Neural recording during retrieval, when participants typically perform an item recognition or source memory task associated with a specific cue, has provided evidence that cortical activity related to modality (auditory or visual)[4, 5], encoding task (imagine or read)[6], or type of odor[7] reactivates during these retrieval tasks. Critically, the reactivation of contextual details during these tests is driven by associative retrieval mechanisms, as only the cue is presented during test. Studies of this nature have shown the reactivation in visual and auditory cortex during the associative retrieval of visual[4, 8-11] and auditory information[4, 5]. These findings of reactivation in sensory association cortex are supportive

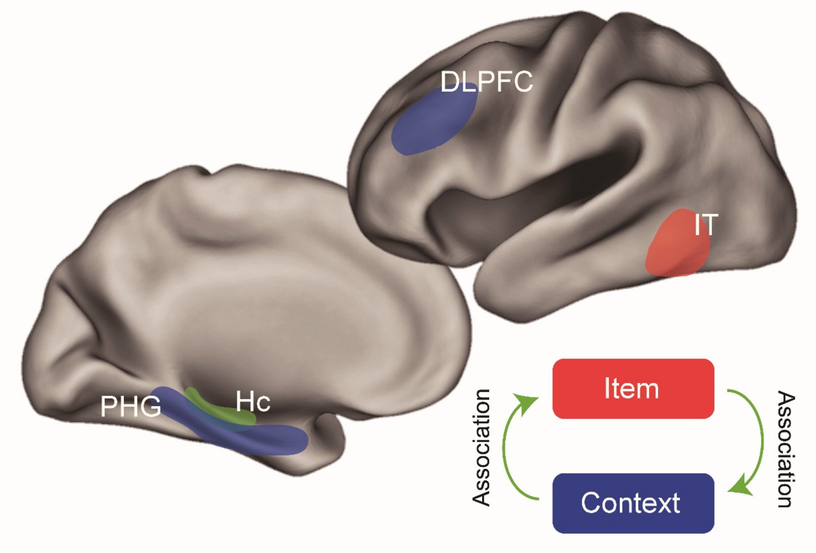


**Figure 1:** *Schematic diagram mapping cortical regions implicated in maintaining and updating context (blue), representing the features of items (red), and forming associations between items and the context in which they are encountered (green).* PHG, parahippocampal gyrus. Hc, hippocampus. DLPFC, dorsolateral prefrontal cortex. IT, inferior temporal gyrus.

of context-based theories of episodic memory, which rely on a representation of item information that activates when a specific item is presented during study, or retrieved through mnemonic processing.

In addition to the activation of associated perceptual information, studies have revealed that activity specific to the type of processes engaged during encoding may also be reactivated during retrieval. Work by Johnson and Rugg[12] demonstrated cortical reactivation in left occipital cortex and anterior fusiform gyrus when participants imagined a verbally presented object in a visual scene, while activity in ventromedial prefrontal cortex was reinstated when the same stimulus was incorporated into a sentence. Work by Kahn and colleagues[6] showed cortical reactivation in the parahippocampal place area (implicated in processing scene information[13]) for imagined items, while items that were read reactivated posterior ventrolateral prefrontal cortex (implicated in lexical tasks). These findings suggest that contextual information beyond sensory perception is bound into episodic memories.

The above neuroimaging studies rely upon the presentation of a cue during test in order to test for the associative retrieval of contextual details. Context-based theories of episodic memory propose that retrieval may occur in the absence of an external cue, as memory search is guided by an internally maintained contextual cue. In support of the contextual reinstatement hypothesis, Polyn and colleagues[14] found cortical reactivation in the visual processing stream during a free recall task. In this study, fMRI data was collected while participants studied images of famous celebrities, locations, or objects, and later retrieved them during a free-recall task. Using multivariate pattern analysis techniques, activity in fusiform gyrus, parahippocampal cortex, and inferior temporal gyrus was shown to reactivate prior to the recall of celebrities, locations, and objects, respectively. These findings are consistent with category-specific activity cuing memory retrieval. In line with the reactivation of task-specific activity in source memory studies, reactivation of task specific activity in occipital cortex, parietal cortex, and lingual gyrus was observed during a similar free-recall task[15.]

Perhaps the most compelling evidence of reactivation of neural activity, driven through the hippocampus, comes from electrophysiological recordings of hippocampal neurons and their surrounding local field potentials from patients with intractable epilepsy. Gelbard-Sagiv and colleagues[16] recorded activity in single neurons of the human hippocampus while patients first viewed cinematic episodes, and later recalled these episodes. A subset of recorded neurons exhibited selective firing throughout

**Free-recall task:**
A memory paradigm in which participants study a list of items on each trial, and are prompted to recall the items in any order, without a retrieval cue.

**Oscillatory activity:** Synchronized activity of a large number of neurons firing at a specific frequency.

**Hebbian learning:** An associative learning process in which connected neurons that exhibit simultaneous firing strengthen their synaptic connections to one another.

the presentation of the encoded materials. Reactivation of these neurons preceded recall of the encoded material, directly linking hippocampal firing and human recollection during memory search. Reactivation of oscillatory activity in the gamma band has also been observed during successful encoding during a free-recall paradigm[17]. This activity, localized to prefrontal, hippocampal, and left temporal lobe electrodes was shown to reactivate during the recall of studied items. Reactivation occurred first within the hippocampus, before the pattern of activity in cortex was reinstated. Findings of this nature are suggestive of recall of past experience originating in the MTL, and propagating to association cortex, where activity reflects the subjective experience of the recollected memory.

**Bridging cognitive models and neural mechanisms**

In the following section, evidence for the neural substrates mediating the major cognitive processes proposed by context-based theories will be briefly reviewed. These theories propose that activity in neocortical association cortex reflects information about individual items recently encountered in the environment. In addition, a context representation contains information about the recent history of items that have been active in association cortex; these theories propose this activity is represented in either prefrontal[18] or parahippocampal[19] regions. Finally, these theories propose that the hippocampus mediates the binding of item and context representations, in the formation of distinct episodes that may be later retrieved. The recall of a specific item, coincident with cortical reactivation of the pattern of neural activity representing said item, is enacted by similar hippocampally mediated Hebbian learning. In this manner, these models provide a means to explain the phenomenon of cortical reactivation during episodic remembering (depicted in **Figure 1**).

Extant neuroimaging evidence speaks to the role of the hippocampus in the successful encoding[12, 20-23] and retrieval [23-26] of episodic memories. There is also a consensus in terms of object representations in association cortex based on modality: superior temporal gyrus for auditory representations, and inferior temporal gyrus for visual representations. Within the ventral visual pathway, specific cortical regions encode specific stimuli, such as the fusiform face area[27], the parahippocampal place area[13], and object responsive areas in lateral occipital cortex[28]. Given the recent advent of context-based theories of episodic memory, limited but promising progress has been made towards identifying potential substrates that mediate a contextual representation. In the following section, evidence supporting parahippocampal cortex activity mediating a temporal context representation will be reviewed. Evidence for the role of the dorsolateral prefrontal cortex (DLPFC) in manipulating, or shaping the information stored in this representation will also be considered.

**Contextual maintenance and integration**

The existence of a slowly changing contextual representation is essential to models of episodic memory. According to the temporal context model[1], changes in context are driven by perceptual inputs to the system, with the similarity of context to prior states decaying in an exponential manner with additional inputs. In order for a region to represent context, patterns of neuronal firing must be capable of changing firing rates based on external inputs (proposed here to reflect perceptual inputs due to feature information), as well as maintain persistent firing over delay periods. Persistent firing enables the maintenance of information in the absence of external stimuli, a critical property of context representations. Persistent firing of cortical assemblies has been recorded in prefrontal cortex[29, 30], limbic regions, including entorhinal cortex[31, 32], perirhinal cortex[33, 34], and lateral amygdala[35] of nonhuman primates and rodents (for a review, see work by Wang[36]).

*Parahippocampal cortex*

Given the firing patterns observed in parahippocampal regions, their afferent sensory inputs, and extensive reciprocal connections to the hippocampus, activity in parahippocampal cortex is well suited to mediate a contextual representation[37, 38]. Studies examining working memory in humans have identified a dissociation between the maintenance of novel information, supported through MTL function, in contrast to familiar stimuli, supported in part by increased prefrontal activation[39]. Similar work has identified that successful encoding of novel visual information is supported by the parahippocampal gyrus[40], which can be reduced through the application of the muscarinic cholinergic antagonist, scopolamine, prior to scanning[41]. Loss of cholinergic modulation, and consequently recurrent firing, to entorhinal cortex also produces reduced encoding of novel, but not familiar odors, in rats[42].

The most compelling evidence for a temporal context representation supported through activity within the MTL comes from recent electrophysiological studies recording from the MTL in humans. Work by Manning and colleagues[43] found direct support for contextual reinstatement, evidenced by the reactivation of oscillatory patterns of brain activity recorded in local field potentials, while patients with intractable epilepsy studied a list of nouns and performed free recall. In their analysis, they identified a slowly changing, autocorrelated signal while patients studied specific items- a contextual representation. Critically, just prior to the recall of individual items, the pattern of contextual activity recorded from temporal lobe electrodes, including the hippocampus, returned to a prior state. Recent recordings from within the MTL have also revealed autocorrelated patterns of neuronal firing, which return to a previous state of firing during a continuous recognition task[44]. These studies build on a growing body of evidence from rodent[45, 46], nonhuman primates[47], and humans[48, 49] for the encoding and maintenance of temporal context within the MTL.

*Dorsolateral prefrontal cortex*

The DLPFC has been proposed to act as central locus for a contextual representation[18, 50], due to its sustained delay period activity in working memory tasks, as well as deficits in source memory[51-53], and recency judgments[54, 55] with frontal lesion pathology (although explicit contextual encoding remains intact in frontal amnesics[56, 57]). Furthermore, patients with frontal lobe lesions have been shown to have spared automatic encoding of temporal information, but deficits in the processing of this information[58]. Functional neuroimaging evidence also points to the role of DLPFC in the selection of action from memory[59, 60] rather than maintenance of information (reviewed by Curtis and D'Esposito[61]). Recent evidence from neural decoding of a prospective memory tasks supports the role of prefrontal cortex in modifying the contents of working memory, which could be decoded in posterior cortical regions (but not task-sensitive regions in anterior and lateral prefrontal cortex)[62]. This top-down modulation of contextual representations fits in line with the temporal patterns of firing in electrophysiological recordings of DLPFC[63], as well as lesions studies of DLPFC and inferior temporal cortex[64]. This evidence speaks to an interactive role of the DLPFC, with a potential role in the organization of information stored in context.

Recent neuroimaging work investigating the role of DLPFC provides evidence for its role in organizing currently active representations held in working memory[65]. In this study, participants encoded a list of three items, and either performed rote rehearsal or reordered the items according to their weight, during a delay period. This reordering task requires additional manipulation of the contents of working memory, as compared to the rehearsal control task. Consistent with the theorized role of DLPFC in the organization of currently maintained representations, activity in DLPFC was greater for reordering, relative to rehearsal, of items in working memory. Increased activity within DLPFC has also been linked to subsequent relational memory effects[66, 67], and subsequent clustering[68] and memory[69] of studied materials during free recall. These findings support a role for the DLPFC in the encoding of associations between currently active item representations; activity in this region may directly interact with inputs to a contextual representation, allowing individual items presented across longer time scales to be associate to similar contextual states. Future studies investigating how activity within DLPFC during working memory tasks influences item representation in posterior cortical regions may provide further insight into the functional role of the DLPFC.

In addition to supporting relational encoding of items, neuroimaging studies of lateral prefrontal cortex function suggest it may mediate temporal context encoding. As previously mentioned, lesions to prefrontal cortex often cause deficits in recency discrimination[54, 70-72]. Motivated by evidence from the neuropsychological domain, Jenkins and

Ranganath[48] examined prefrontal and MTL contributions to the encoding of temporal-order memory. In this study, participants encoded a series of four stimuli, and after an eight second delay, were required to indicate from which position a test probe was encoded in the list. Activity during trials in which subjects correctly assessed the position of the probe was compared to activity during incorrect trials. This contrast of fine temporal memory encoding revealed activity in parahippocampal cortex. In addition to this within-trial measure of temporal context encoding, participants were given a post-scan test in which they indicated the temporal position an item was presented in on a time line representing the duration of the experiment. Activity in rostrolateral prefrontal cortex, DLPFC, and anterior hippocampus promoted the encoding of coarse temporal memory. To test if the pattern of activity in any of these regions represented a gradually changing contextual representation, a multivariate pattern analysis of activity in regions showing temporal memory effects was conducted. In this analysis, patterns of activity were constructed in each region of interest, and the similarity of these patterns was compared to adjacent trials. Trials with accurate coarse memory were associated with a dissimilar pattern of activity, relative to neighboring trials. If this pattern of activity in fact represents the encoding of temporal context, the distinct temporal context may facilitate subsequent temporal order judgments. Alternatively, if items are encoded with similar contextual states, it may be more difficult to distinguish when they occured, relative to other items in the list. These findings, as well as other reports of DLPFC activity supporting subsequent temporal order memory in similar studies[49] supports the role of prefrontal processes in supporting the encoding of temporal context.

## Conclusion

Recent findings suggest that activity in the MTL may mediate a contextual representation, critical for episodic memory. The manner in which information is gated into the medial temporal lobe may be controlled by activity in prefrontal frontal cortex, allowing for control over the current contextual representation. Future studies should emphasize how interactions between prefrontal cortex and the medial temporal lobe shape the current state of context.

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Correspondence: james.e.kragel@vanderbilt.edu

Further information: http://www.vanderbilt.edu/allylab