

# The role of the hippocampus in memory and mental construction

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Much has been learned about the processes that support the remembrance of past autobiographical episodes and their importance for a number of cognitive tasks. This work has focused on hippocampal contributions to constructing coherent mental representations of scenarios for these tasks, which has opened up new questions about the underlying hippocampal mechanisms. We propose a new framework to answer these questions, which incorporates task demands that prompt hippocampal contributions to mental construction, the online formation of such mental representations, and how these demands relate to the functional organization of the hippocampus. Synthesizing findings from autobiographical memory research, our framework suggests that the interaction of two task characteristics influences the recruitment of the hippocampus: (1) the degree of task open-endedness (quantified by the presence/absence of a retrieval framework) and (2) the degree to which the integration of perceptual details is required. These characteristics inform the relative weighting of anterior and posterior hippocampal involvement, following an organizational model in which the anterior and posterior hippocampus support constructions on the basis of conceptual and perceptual representations, respectively. The anticipated outcome of our framework is a refined understanding of hippocampal contributions to memory and to the host of related cognitive functions.

**Keywords:** hippocampus; autobiographical memory; episodic memory

## Introduction

A relatively new trend in autobiographical memory research is to illustrate how the processes supporting detailed remembering help create other mental experiences.<sup>1–4</sup> Although this movement has a history that dates back to the time of William James<sup>5</sup> and Frederic Bartlett,<sup>6</sup> recent interest has focused heavily on the similarities within the neurocognitive machinery that support both autobiographical memory and a range of tasks requiring complex mental representations, from manifesting a sense of self<sup>7–9</sup> to influencing social interactions and empathic responses,<sup>10,11</sup> and to supporting goal-directed tasks such as planning and solving complex problems.<sup>12–14</sup> Guided by the essential role of the hippocampus in autobiographical memory, this research has focused on how the hippocampus contributes to these multiple forms of mental creation (for recent reviews, see Refs. 15–17).

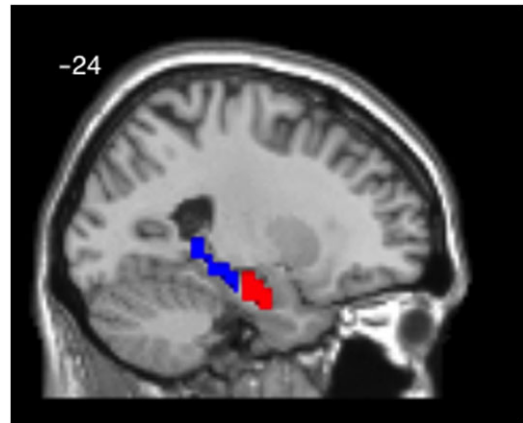
Although the key role of the hippocampus in memory has been established for over 50 years, the precise mechanism of hippocampal function across various cognitive tasks remains a topic of debate. One view that extends from cognitive map theory<sup>18</sup> and the discovery of place cells within the hippocampus<sup>19</sup> is that the hippocampus is specialized in processing spatial information. Another view posits that the role of the hippocampus is not exclusive to space, but is fundamental for storing and relating together all forms of information from memory.<sup>20–22</sup> According to the latter view, spatial representations are just one example of the types of relational processes that are supported by the hippocampus.

These theories have been directly applied to autobiographical memory research in order to understand how the processes that support remembering relate to other cognitive domains.

The scene construction theory<sup>23–25</sup> suggests that when one is thinking about past events, the hippocampus constructs a scene as a method of packaging information. Once these scenes are generated, details of a remembered event can be integrated, and these same processes can be used to form imaginative scenes to guide behavior, such as bringing to mind future and novel scenarios. Aligning with the broader relational processing account of the hippocampus, the constructive episodic simulation hypothesis<sup>14,15,26</sup> suggests that hippocampal processes support autobiographical memory in a flexible manner, binding together multiple details of an event. These processes can build new event simulations, not just scene-based imaginations, by recombining the details accumulated from several past events to support tasks such as problem solving, planning, and creativity.<sup>12,27–31</sup>

The central proposition of both scene construction and constructive event simulation is that the processes of the hippocampus are not confined to remembering. This proposition has prompted interesting new questions about how and when the hippocampus contributes to retrieval scenarios beyond remembering, particularly queries into how remembering and related tasks influence the placement and mechanistic activity within the hippocampus. We argue that current views are limited in addressing these questions because they focus on the hippocampus as a homogeneous structure or on one aspect of the hippocampus (e.g., see Ref. 32). It is clear from animal models and laboratory studies of memory that there is a division of labor along the longitudinal axis of the hippocampus.<sup>33,34</sup> Thus, a refined model of hippocampal contributions to autobiographical memory and related retrieval is necessary.

We propose a refined framework that integrates key aspects of the above-mentioned theoretical accounts with evidence of the types of retrieval demands that activate the hippocampus, as well as neuroimaging findings that specify the location of the underlying hippocampal activity with respect to the long axis (from the anterior to the posterior hippocampus; Fig. 1).<sup>34</sup> We present this approach as a framework in which the hippocampus is chiefly involved in mental construction, the online mental creation of scenarios. According to this framework, the manner in which the hippocampus carries out mental construction is determined by task


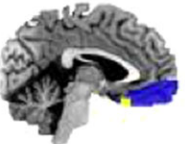

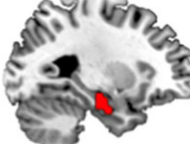






**Figure 1.** An example of left anterior (red) and posterior (blue) hippocampal segments from a single subject on a T1-weighted standard template.

demands, particularly when they are such that there is no established retrieval framework and/or there is a required configuration of perceptual details upon construction, which will predict where along the hippocampus activity is concentrated.

Our framework allows for speculation on how these demands will predominately engage different computations of the hippocampus, namely pattern-separation and -completion mechanisms, along the long axis.<sup>35–38</sup> The hippocampus is known to engage pattern separation to encode events as unique codes, whereas pattern-completion mechanisms use a portion of an existing representation to reactivate stored details (for a review, see Ref. 37). In this paper, however, we will discuss these computations only as a trend for future research, given the limited work in this area (see discussion below on future directions), and will instead focus on the demand and functional hippocampal organization aspects of our framework.

This new framework for hippocampal contributions to mental construction, illustrated in Figure 2, is guided by three important principles. First, as noted, this framework is not intended to replace existing theoretical perspectives. Rather, it is an integration of existing theories with new perspectives on retrieval demands and the organization and computations of the hippocampus. Second, our framework does not discriminate between constructions on the basis of the task (i.e., remembering, navigating, or imagining) or consider such tasks as unitary. Instead, our framework

		<i>Framework for retrieval</i>	
		Present (well-defined task)	Absent (open-ended task)
Perceptual details	Not required	 <p><b>Construction form:</b> None, recalling existing script or schema</p>  <p><b>Nonhippocampal structures:</b> VMPFC temporal cortices</p>	 <p><b>Construction form:</b> Conceptual</p>  <p><b>Hippocampal localization:</b> Anterior hippocampus</p>
	Required	 <p><b>Construction form:</b> Perceptual</p>  <p><b>Hippocampal localization:</b> Posterior hippocampus</p>	 <p><b>Construction form:</b> Conceptual and perceptual</p>  <p><b>Hippocampal localization:</b> Anterior and posterior hippocampus</p>

**Figure 2.** The proposed framework for mental construction in which the interaction of two retrieval characteristics—open-ended task demands and the requirement of perceptual details—predict the engagement of the anterior and posterior hippocampus in forming mental representations. This figure uses the metaphor of constructing a house to illustrate when and how the hippocampus will contribute to mental representations via construction. Top left quadrant: when retrieval is well defined (i.e., when there is a framework or schema for retrieval, illustrated here as a frame or building blocks of a house), a general mental representation can be completed by recalling schematized information. This is supported by nonhippocampal processes and thus does not require any hippocampal mechanisms. Bottom left quadrant: when the general framework that is retrieved via established schemas is not detailed enough for the current task, posterior hippocampal mechanisms will be recruited to complete the framework with additional perceptual details. Top right quadrant: when retrieval is open ended, for example, in cases in which there are no such frameworks or schemas to guide what to retrieve, the anterior hippocampus is required to form a mental construction of a conceptual or goal-oriented framework. With respect to the house metaphor, the anterior hippocampus must construct this framework with existing conceptual information (the lumber). Bottom right quadrant: when these newly formed conceptual frameworks for open-ended tasks (constructed via the anterior hippocampus) require fine-grained perceptual details beyond what was generated by the anterior hippocampus, mechanisms of the posterior hippocampus will revive details of past scenarios.

focuses on the online processing requirements of all forms of mental construction that are determined by retrieval demands. Third, our framework does not view the hippocampus as a unitary structure: it incorporates functional–anatomical distinctions within the hippocampus as a means of organizing discriminant forms of mental construction along the longitudinal axis. Figure 2 illustrates these points, which we use to guide the reader through our framework.

To build this framework, we leveraged research on autobiographical memory, the most thoroughly studied and prototypical example of mental construction in human subjects, which specifies the task demands that recruit the hippocampus. We then use the knowledge gained from functional specialization within the hippocampus (e.g., see Refs. 33, 34, and 39) to argue that the anterior hippocampus is preferentially involved when a construction must converge onto a conceptual representation, and the

posterior hippocampus is preferentially involved when a construction must converge on, or configure, a perceptual representation.

To establish this framework, in section one, we define hippocampus-mediated mental construction. We argue that autobiographical memory retrieval, when dominated by episodic memory (e.g., recalling contextual details of the past), is the paradigmatic case of mental construction and can thus be used to distinguish between hippocampal and nonhippocampal forms of mental representation.<sup>40–42</sup> In doing so, we show that when mental representations must be constructed online, the hippocampus acts as a zone of convergence for coordinating details into cohesive constructions. In section two, we evaluate the particular retrieval scenarios, from behavioral and neuroimaging findings, that recruit the hippocampus to act as the zone of convergence for mental constructions. We posit that the hippocampus mediates mental constructions when a task demands a representation be built under open-ended or ambiguous conditions (i.e., tasks without retrieval frameworks) or when specific perceptual details must be included. As such, the hippocampus is not necessary when an existing framework of knowledge can be used to generate a representation. Finally, in section three, we indicate how the relative weighting between these two retrieval characteristics will determine the nature of hippocampal contributions, attending to the location of activity along the longitudinal axis of the hippocampus.

### Section one: mental construction

Mental construction—whether for remembering past events or for novel scenarios that can guide future behavior—is the online integration of multimodal informational details into a central construct to form a coherent representation. This definition encompasses two key principles, the first of which is that mental construction requires a core concept to act as a type of “cognitive glue” that can bind together associated details to create a cohesive representation. Much like following a new recipe or building furniture requires a central construct or goal (e.g., a cake or a cabinet), so do mental constructions. The second principle is that this “glue” is required to combine at least two disparate forms of information online.

These principles are supported by a host of laboratory studies that have shown how the hippocampus reinstates relations among distinct elements of an experience upon retrieval.<sup>43–46</sup> For example, neuroimaging studies have demonstrated the preferential involvement of the hippocampus for retrieving item–context memory relations, but not for retrieving single items. The hippocampus specifically contributes to recognition memory paradigms that depend on relating details reflecting contextual and spatial information, whereas nonhippocampal medial temporal lobe (MTL) cortical structures contribute to item-based recall.<sup>21,47,48</sup> Concordant findings from animal models have also shown that dissociable mnemonic processes are supported by different structures within the MTL.<sup>44,49–52</sup>

These findings suggest that when a task requires a representation to be formed around a central construct with multiple details, it then requires mental construction and, in turn, the hippocampus. We apply this definition to autobiographical memory retrieval (the preeminent form of mental construction) to illustrate when and how hippocampal processes contribute to various forms of retrieval.

#### *Hippocampal contributions to autobiographical memory*

As a mental construction task, remembering an autobiographical event requires relating together many disparate forms of information. A common distinction within autobiographical memory is between information that belongs to the domains of episodic versus semantic memory.<sup>53</sup> Episodic memory involves recalling unique details of an event, including context-specific information (“where,” “what,” and “when”). Semantic memory involves recalling facts and information, both about the self and the world, which are related but not exclusive to the remembered experience. The relative weighting of these components determines how an autobiographical memory is constructed and experienced, as well as the extent to which it is hippocampus dependent.

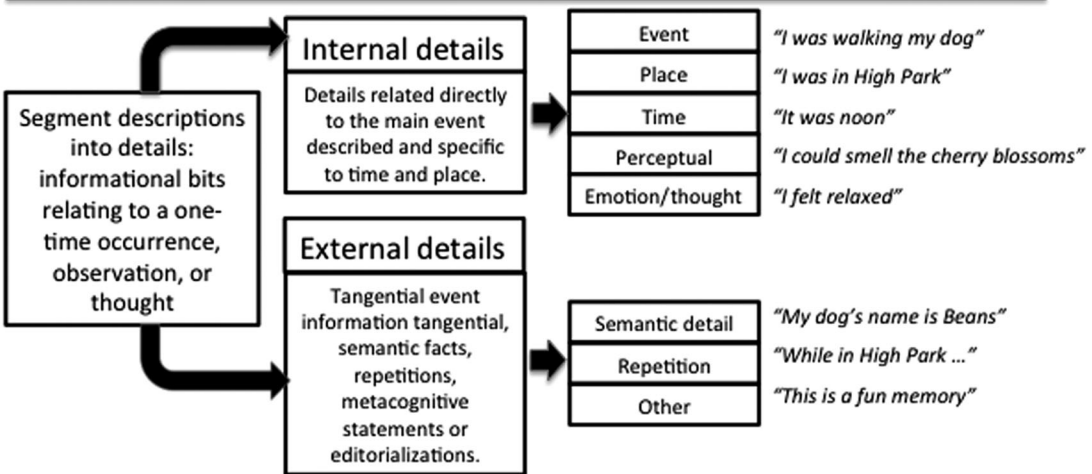
According to a prominent theory of hippocampal function, the multiple trace theory (MTT) of memory<sup>54</sup> (for an update, see Refs. 55 and 56), hippocampal involvement in a task is determined by the degree to which episodic memory is required. When an event is remembered by

## The autobiographical interview

### Administration

Describe a one-time experienced event in detail	Free recall	General probe	Specific probe
	Speak about the event without any interruption from the examiner.	Non-specific statements or instructions are given	Highly-structured interview designed to elicit additional contextual details
<i>"Walking my dog for the first time."</i>	<i>"A month ago, I was walking my dog in High Park ..."</i>	Experimenter: <i>"Can you remember anything else?"</i>	Experimenter: <i>"Tell me more about objects / thoughts/ etc.?"</i>

### Scoring



**Figure 3.** The autobiographical interview (AI). Administration: the standard administration requires participants to generate one-time experienced events. Once these events are selected, participants are asked to describe them in as much detail as possible. During the initial free-recall phase, participants speak about the event without any interruption from the examiner. During a general probe phase, nonspecific statements or repetitions of the instructions are given to encourage greater recall of details or to focus on a single, specific event. During the specific probe phase, a highly structured interview designed to elicit additional contextual details is given. The AI method remains valid at all levels of retrieval; thus narratives can be assessed after free recall or investigated after the facilitative effects of the probe trials. Scoring: to score the descriptions, narratives are segmented into details—informational bits relating to a one-time occurrence, observation, or thought—and these details are classified as either internal, if they relate directly to the main event described and are specific to time and place and therefore episodic in nature, or external, if they contain event information tangential or unrelated to the main event, semantic facts, repetitions, or other metacognitive statements or editorializations. Internal and external details can be further categorized (as illustrated); however, the overall number of internal details provides a main measure of episodic recollection and level of episodic specificity. This scoring technique remains valid when applied to memory and nonmemory narratives and descriptions that are collected using modifications of the administration protocol.

recombining multiple episodic elements of an event, construction will require the hippocampus. Strong support for the specialized involvement of the hippocampus in mnemonic episodic mental construction comes from behavioral investigations that have used semistructured interviews and asso-

ciated scoring techniques to measure detail in past personal memories.<sup>57–59</sup> For example, in the standard administration of the autobiographical interview (AI; Fig. 3),<sup>60</sup> participants describe past personal events. These descriptions are segmented into details, which are then classified to capture the

episodic and semantic components of the autobiographical memory narrative. Internal details are those that are contextually specific to the described event, relating to components of episodic memory (e.g., “I wore a red dress”; “We sat in a tight corner of the Italian restaurant”). External details are pieces of information that are not specific to the described event, including semantic information, as well as editorial statements, details about other events, and repetitions (e.g., “I love wearing red”; “I have always loved Italian food”).

Studies of aging and patients with hippocampal damage have illustrated the necessity of this structure for recalling and combining episodic (internal) details during autobiographical retrieval. Age-related memory impairment is specific to episodic memory, with semantic memory processes remaining largely stable with age, a pattern that has been attributed to volume reductions in the hippocampus. Using the AI, there is a selective age-related deficit in the recall of internal details, whereas external details are increased with age.<sup>61</sup> Older adults remember the general gist of a memory and associated facts (i.e., recalling a schematic mental representation), but they do not construct events in specific detail (i.e., mental construction) to the same degree as younger adults, a finding replicated numerous times.<sup>12,26,29,62</sup> A selective deficit of internal detail generation has been documented in a host of other conditions marked by MTL atrophy or excisions, including mild cognitive impairment (MCI), which specifically affects episodic memory owing to alterations of the MTL,<sup>29,63–65</sup> and temporal lobe epilepsy (TLE) involving excised or atrophied hippocampi.<sup>66–69</sup> There is selective hippocampal involvement in constructing and integrating internal details; patients with focal hippocampal damage produce fewer internal, but not external, details when constructing events<sup>70</sup> (for an exception, see Ref. 71).

Neuroimaging studies have also established the engagement of the hippocampus during episodic construction of autobiographical memories with multiple details. Detailed event recall, as assessed by the AI, has been associated with sustained hippocampal activity.<sup>69,72</sup> Hippocampal activity during autobiographical memory has also been linked to subjective vividness ratings,<sup>73–75</sup> the hallmark of perceptual detail integration (i.e., combining together multiple details), even for memories that

are rehearsed and from different time periods of an individual’s life span.<sup>76,77</sup>

In cases in which autobiographical memory recall does not draw upon episodic memory processes, the hippocampus is not preferentially involved. These memories are recalled by remembering a schematic or existing framework of an event and are therefore not constructed online. According to the MTT, extracting the commonalities among the repeated constructions, or rehearsals, of an event over time forms a semantic representation of that scenario. The retrieval of these complex semantic representations does not require binding disparate details of the scenario. According to our framework, these mental representations do not require reconstruction because they can use existing schematic information (Fig. 2, top left quadrant). Instantiating these forms of mental representations via well-rehearsed schemas (such as “going to the doctor” or “brushing your teeth”) relies on the ventral medial prefrontal cortex to act as the hub for storing these schemas and for subsequent mental representation retrieval.<sup>78,79</sup> Support for our view is derived from the fact that patients with developmental amnesia due to hippocampal damage are able to use intact semantic or scripted frameworks to describe atemporal scenes, although these are not as vivid or perceptually rich as scenes described by participants with intact hippocampi.<sup>80</sup> Furthermore, those with hippocampal lesions are able to bring to mind and describe schematic routes of a familiar environment, but not details of that description (see Ref. 81 for a view related to this section).<sup>82</sup>

Thus, not all mental representations recruit the hippocampus; the hippocampus is only required when such representations are the result of construction. As illustrated in Figure 2, mental construction can rely on different types of hippocampal processing, depending on the demands of the task. Our framework specifies the precise retrieval demands, both with respect to memory and other cognitive domains, which require different constructive hippocampal processes.

## Section two: retrieval scenarios that recruit the hippocampus

As noted above, a number of studies show that the same hippocampal processes that are required for constructing autobiographical memories are also required for generating detailed future or imagined

scenes and scenarios.<sup>2,15,16,23,83,84</sup> Over the past 30 years, there have been numerous reports that hippocampal damage leads to corresponding deficits in remembering the past and imagining the future, highlighting the concomitant role of the hippocampus in construction scenarios, regardless of their placement in time with respect to the past and future.<sup>83,85,86</sup>

Studies of this sort can be used to extract commonalities in retrieval demands that will recruit the hippocampus. These scenarios are based on the interaction between two critical characteristics of autobiographical memory that have been reported to induce hippocampal activity: (1) the requirement for the integration or arrangement of two or more perceptual details, and (2) that retrieval is relatively open ended (Fig. 2). These characteristics define our prototypical example of mental construction, episodic autobiographical memory. The hallmark of episodic autobiographical retrieval is the self-generation of specific event-unique details (traditionally defined as the “what,” “where,” and “when”) that cannot be retrieved solely from general knowledge.<sup>53</sup> As an open-ended task, autobiographical memory does not have a set routine or framework for remembering, and task demands can change depending on the retrieval context.<sup>3,87</sup> A broader definition of open-ended tasks are those in which there are typically multiple different ways to perform the task, with multiple possible satisfactory outcomes that can change according to task demands.<sup>88</sup> This is in contrast to closed-ended or well-defined tasks that have a single anticipated outcome if a set path is followed.<sup>29</sup> In the next section, we provide evidence that the interaction of these two characteristics upon retrieval—generating and integrating details, and open-endedness—will engage hippocampus-mediated mental construction mechanisms. This is followed by a discussion on how these characteristics can predict hippocampal functional localization.

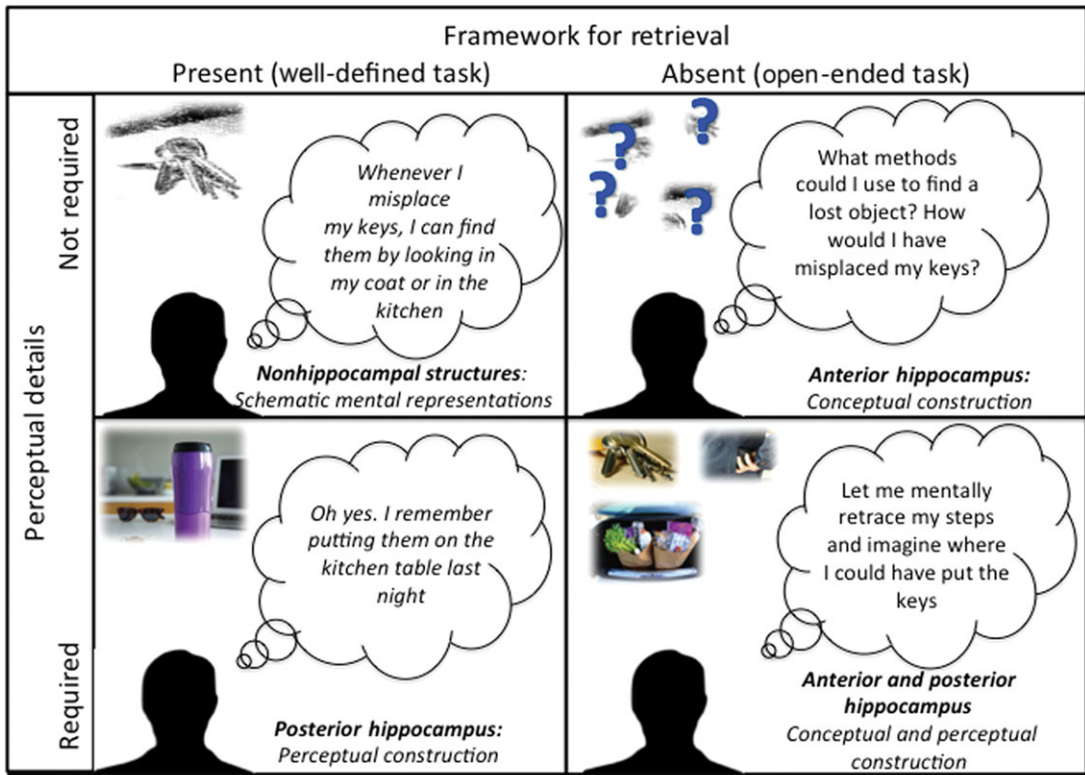
### *A requirement of perceptual detail*

Forming mental representations from prototypical or schematic knowledge (i.e., recalling an existing knowledge framework) does not require the hippocampus (Fig. 2, upper left quadrant). For example, as illustrated in Figure 4, if misplacing your keys is something that happens quite often, you likely have a script or schema related to finding

your keys. When you discover that your keys are lost and cannot remember where you last put them, retrieving the scripted framework (e.g., that your keys may be in your coat pocket and the steps you would take to look for your keys) can be supported by nonhippocampal structures (Fig. 4, upper left quadrant). Supporting evidence for this idea comes from reports on patients with TLE who had experienced hippocampal atrophy (presurgical) or resected hippocampal and extrahippocampal structures. In one study, these patients were assessed using the AI and a script-generation task in which they described familiar activities, such as eating at a restaurant, washing dishes, or grocery shopping. Although both groups of TLE patients generated impoverished autobiographical memory recollection relative to the comparison group, script-generation performance was intact when damage was confined to the hippocampus.<sup>66</sup>

According to our framework (Fig. 2, lower left quadrant), if the specificity of the recalled knowledge framework is insufficient for retrieval, then hippocampal mechanisms will be recruited to fill in the representation with more details. Race and colleagues asked MTL-lesion patients to think about issues related to the public (e.g., issues facing your community). Whereas the patients could list these issues in general, drawing upon a general knowledge base, they were unable to elaborate on them in detail.<sup>89</sup> Rabin and colleagues<sup>90</sup> reported similar results on a theory-of-mind test in a single case of hippocampal damage in developmental amnesia. They presented the patient with photographs of someone who is familiar (personal theory of mind), unfamiliar (general theory of mind), or from their own history (episodic memory). The patient was not impaired in the unfamiliar condition; they could rely on general scripts or mental models to complete the task, but they could not perform the task at the same level of detail as control subjects. When additional details were required to construct specific details of their acquaintances, the patients were impaired relative to comparison participants. These findings serve as evidence that the hippocampus is not necessary when retrieval is associated with a general rule, unless additional specifications or details need to be generated and integrated into the established information (e.g., detailed retrieval). Returning to the example relating to misplaced keys, recalling a schema for finding

## The case of the missing keys



**Figure 4.** The concepts of construction proposed by the above framework are illustrated with the example of retrieving the location of lost keys. Top left quadrant: upon noticing that your keys are misplaced, you recall a typical script that you use to find your often-lost keys, without reference to a specific percept. This form of retrieval does not require the hippocampus. Bottom left quadrant: if you can recall where you put your keys by reviving the specific location where you left them (e.g., on your kitchen counter), posterior hippocampal mechanisms will construct this scenario via the reconstruction of fine-grained perceptual details. Top right quadrant: if such a memory or script is insufficient, then the task becomes more ambiguous. In this case, you can think about related concepts, the methods used to find lost things, or goals and motivations to create a conceptually based construction that recruits the anterior hippocampus. Bottom right quadrant: if this conceptual construction is not detailed enough, posterior hippocampal mechanisms will be recruited to retrieve specific details to form detailed scenarios, such as imagining retracing your steps.

one’s keys may not be sufficient; it may be necessary to draw upon hippocampus-mediated processes to embellish this schema with additional perceptual details, thus reinstating a memory (Fig. 4, lower left quadrant; for related work examining the role of schemas/scaffolds on mental construction tasks such as future imagination, see Refs. 91–93).

### Open-ended task demands

Our framework suggests that mental construction under ambiguous or open-ended task demands requires hippocampal processes (Fig. 2, upper and lower right quadrants). This scenario is differenti-

ated from well-defined tasks (e.g., finding misplaced keys) or recalling a highly familiar event that has been recounted numerous times (e.g., one’s wedding day or other personal folklore) that entail unified representations. Without an existing schema, these tasks must rely on flexible hippocampal processes to mediate the online formation of novel, goal-oriented, and coherent representations.<sup>94</sup> For example, if one does not often misplace keys, finding them, if they are lost, is an ambiguous task and requires additional conceptual processes, possibly embellished with perceptual details (Fig. 4, right). A way to solve this task is to think of how one would



lose items such as keys (conceptual) and then use these concepts to guide one's search, and perhaps also connecting a goal of finding the keys with details, and engaging the flexible recombinatory mechanisms of the hippocampus to form precise examples of where the keys may be (e.g., mentally tracing steps) (Fig. 4, lower right quadrant).

One prevalent form of open-ended retrieval is social problem solving (e.g., making friends in a new neighborhood), which we used to test the idea that the hippocampus specifically supports open-ended construction. To do so, we gave older and younger adults, as well as patients with TLE and healthy comparison subjects, a test for open-ended social problem solving, using the means-end problem solving (MEPS) test. The MEPS test contains 10 vignettes that consist of a social problem for which a participant is asked to describe the ideal solution. When we scored the narratives for effectiveness by counting the number of steps they described to get from problem to solution state, two groups, the older adults and patients with TLE, generated less effective solutions. Critically, when these narratives were scored with the AI, older adults and TLE patients provided fewer internal, but not external, details compared to their matched counterparts.<sup>12</sup> The correspondence of hippocampal functioning with generating solutions to open-ended problems did not extend to well-defined tasks.<sup>95</sup> We also found this pattern in amnesic MCI.<sup>29</sup> Following our studies, Madore and colleagues used a training induction task that selectively targeted episodic processes mediated by the hippocampus to show that this type of training positively affected performance on the MEPS test. This was seen both for measures of effective problem solving and specificity (e.g., internal detail generation), a pattern that mimicked performance on memory and imagination tasks following episodic induction.<sup>96–98</sup>

Beyond the wealth of support for hippocampal involvement in open-ended problem solving, others have found that the hippocampus plays a pivotal role in creative mental constructive tasks that are also open ended in that they require building representations under ambiguous retrieval situations. These tasks have included creative language use,<sup>28,99</sup> as well as divergent and creative thinking. For example, in a recent study, patients with MTL damage demonstrated impairments relative to comparison subjects at generating hypotheses about improbable

situations and creating novel drawings from basic shapes (e.g., an oval).<sup>30</sup>

In summary, the recruitment of flexible hippocampally supported mental-construction processes is required for both open-ended tasks and tasks requiring detailed retrieval. Up until this point, we have discussed the hippocampus as a unitary structure, but a critical aspect of our framework is that it incorporates functional heterogeneity within the hippocampus. This heterogeneity can further distinguish hippocampal contributions to mental construction on the basis of these retrieval demands.

### Section three: hippocampal functional organization

Different segments of the hippocampus, particularly the anterior and posterior segments, roughly corresponding to the head and body/tail of the hippocampus (Fig. 1), are engaged by different processing characteristics of mental construction. Functional segregation along the longitudinal axis of the hippocampus has received strong support from structural connectivity studies in animals and humans.<sup>39</sup> These studies have suggested that anterior aspects of the hippocampus send and receive input from areas including the dorsal and medial prefrontal cortices, and the amygdala and lateral temporal cortex, while the posterior aspects of the hippocampus have projections mainly to the mammillary bodies, anterior thalamus, and retrosplenial cortex, and receive input from the posterior cingulate and the occipital and temporal cortices.<sup>100</sup> More recent reports have confirmed anterior and posterior hippocampal structural patterns in humans with tractography-based parcellation and resting-state connectivity.<sup>101</sup> These divisions in pathways to the hippocampus provide a neuroanatomical basis for distinct functional cortical communication patterns. Accordingly, there is evidence for intrinsic functional connectivity between the posterior hippocampus and posterior midline cortical structures and between the anterior hippocampus and lateral temporal cortex, temporal pole, and anterior midline structures, such as the ventral medial prefrontal cortex.<sup>102</sup> These studies suggest that the anterior and posterior aspects perform disparate functions when retrieving (and encoding) information.

One of the more prominent models to explain this distinction of hippocampal function is a gradient-based model,<sup>33,103,104</sup> in which

hippocampal relational processes can bind together coarse details as well as perceptual contextual details. These different resolutions of relational details determine the location of hippocampal activity along the long axis.<sup>34,105–107</sup> A common interpretation of this model is that the anterior hippocampus is recruited for coarse-based information, such as recovering general emotional information or object-based conceptual information, whereas the posterior hippocampus is critical for retrieving fine-grained perceptual or geometrically based relations, such as the location of a landmark in space or particular temporal sequences.<sup>108–110</sup> Alternate but not orthogonal views are that the anterior and posterior aspects process familiar versus contextual details of events.<sup>111–113</sup>

Within our framework, these findings and formulations can be used to predict how hippocampal segments will support mental construction on the basis of the noted retrieval characteristics of construction. We suggest that the anterior hippocampus is preferentially involved when a construction must converge onto a conceptual representation, and the posterior hippocampus is preferentially involved when a construction must converge around perceptual details (for related commentary, see Ref. 114).

#### *Anterior and posterior hippocampal contributions to mental construction*

Open-ended retrieval demands (e.g., solving the social problem of a sparse friend group; planning a vacation) that require establishing a goal or concept (e.g., “How do I make friends?” or “What kind of vacation do I want?”) as the driving force of construction will recruit the anterior hippocampus to create the mental construction (Fig. 2, upper right quadrant). As previously noted, open-ended scenarios are not associated with knowledge structures, which is why mental construction must begin by internally establishing a conceptual goal or motivation (answering the question at retrieval of “What must I construct?”). The conceptual goal acts as a node of convergence for the hippocampal-cortical connections to retrieve the elements needed to build the construction. The above-mentioned connections of the anterior hippocampus with areas of the brain that support high-level perceptually free conceptual information, such as the ventral and lateral temporal lobes as well as prefrontal cortical regions, suggest that the anterior hippocampus is

a likely convergence zone for recovering and integrating conceptual information.<sup>115,116</sup> The notion of the anterior hippocampus as a conceptual node of convergence is also supported by the discovery of “concept cells” in this region<sup>117</sup> and the link between anterior hippocampal activity to novelty, reward, and emotion processing,<sup>118–120</sup> all of which underlie goal formation, particularly in open-ended scenarios. The anterior hippocampus is also preferentially recruited when there is a demand to integrate novel and associative information<sup>121,122</sup> and to establish links between conceptual information.<sup>123</sup> For example, the perirhinal cortex, which feeds its main projections into the anterior hippocampus, is crucial for retrieving conceptual object information,<sup>124</sup> and the anterior hippocampus is more active for familiar information that can converge relations onto a concept.<sup>125,126</sup>

When a mental construction is triggered and subsequently created around externally derived perceptual details, however, the posterior hippocampus will be recruited, regardless of whether it is an open-ended or well-defined task (Fig. 2, lower left and right quadrants). This form of construction is typically based on imagery-guided information recruited via sensory or perceptual representations rather than the above-mentioned conceptually guided information (Fig. 4, lower right quadrant). The notion that the posterior hippocampus supports such forms of mental construction comes from spatial processing research. Perhaps one of the more seductive examples of the involvement of the posterior hippocampus in configuring specific spatial representations is the finding that an enlarged posterior hippocampus in relation to the anterior hippocampus is critical for configuring specific representations in London taxi drivers who must create specific maps of the city in order to navigate.<sup>127</sup> Similarly, Poppenk *et al.* found that posterior hippocampal size is related to recollection and source memory, which relies on details.<sup>128</sup> Functional neuroimaging studies have reported that posterior aspects of the hippocampus support generating fine-grained spatial information or retrieving or constructing detailed spatial representations.<sup>103,110,129</sup> Beyond spatial construction, the posterior hippocampus is involved in a host of other tasks that require relating together specific experienced details. Indeed, there is now evidence that the posterior hippocampus supports

fine-grained representations, even when these occur in temporal “space”<sup>108,109,130,131</sup> (for recent views on this topic, see Ref. 132).

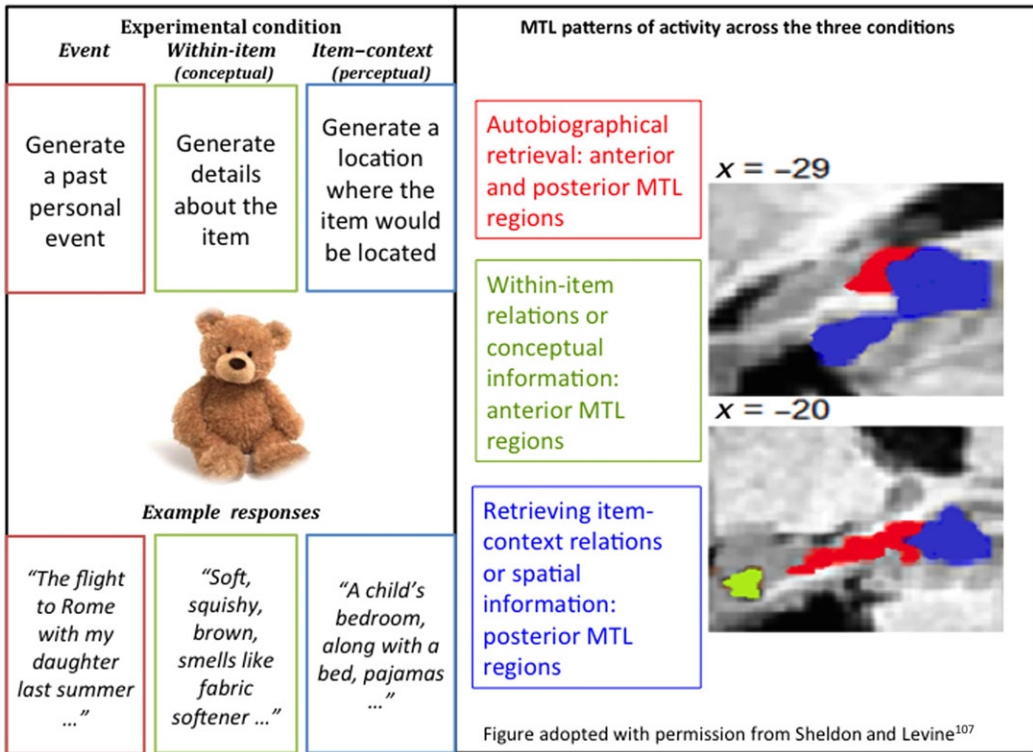
There is support for our framework’s view of anterior and posterior hippocampal processing from the handful of studies that have directly compared the contributions of these hippocampus subregions to construction-like tasks. For example, Evensmoen and colleagues<sup>104</sup> found that during spatial construction tasks, participants recruited the anterior hippocampus when recalling coarse environmental information, but recruited the posterior hippocampus for more specific direction judgments (also see Ref. 103). Some of the strongest evidence comes from neuroimaging studies examining the time scale of hippocampal involvement during autobiographical memory retrieval. These studies indicate that an anterior hippocampal circuit is preferentially recruited during memory construction (accessing concepts), and posterior hippocampal circuits are preferentially recruited at later time points of autobiographical memory retrieval, when perceptual details of an event are recalled.<sup>133,134</sup> In accordance with these notions, a meta-analysis showed that direct episodic access to memories with an accompanying sense of (high-imagery) remembering recruited the posterior hippocampus to a greater extent than accessing memories without such direct and strict access, thus relying more strongly on conceptual integration.<sup>135</sup> A recent functional magnetic resonance imaging study had a group of participants imagine future events for the first time versus recall events that they had already imagined, with greater activity in both the anterior and posterior hippocampus for the imagine condition, reflecting the use of conceptual and perceptual construction. Interestingly, when a baseline task that involved pleasantness ratings for a presented set of features was used, only posterior hippocampal activity differences between the conditions remained. Although the authors used this baseline to control for novelty encoding, it is also possible that the baseline controlled for conceptual construction, given that the pleasantness ratings involved accessing and integrating conceptual information about attributes, thus fitting with our framework.<sup>136</sup>

We recently reported the results of a neuroimaging experiment that tested the neural correlates of mental construction activities. In response to pictures of objects, participants retrieved information

under three conditions. They were asked to generate conceptual information by retrieving relations among features of a pictured item (within-item relations; e.g., features of a fridge—its look, feel, function, and size) to configure perceptual spatial information around that item, retrieving relations among items in a context (item–context relations; e.g., the fridge is in the kitchen), or to mentally construct a past autobiographical memory (Fig. 5). Using multivariate analyses, we found dissociable patterns of activity within the MTL and hippocampus for these forms of construction. Autobiographical event construction recruited the hippocampus along the entire length of the axis; construction that required conceptual information (within-item relations) recruited the anterior hippocampus; and construction that required specific contextual information (i.e., perceptually based; item–context relations) recruited the posterior hippocampus, thus supporting our proposed distinction.

### **Concluding remarks: the next trends in autobiographical memory research**

The current trend in autobiographical memory research has been to document how the same processes used to mentally construct detailed past events also serve mental construction under various retrieval scenarios, from social interactions to planning and problem solving. In the past few years, several theories, namely the scene construction theory and the constructive event simulation theory, have been advanced to explain how hippocampal processes are central to all forms of mental construction, which have helped elucidate the breadth of hippocampal contributions to tasks beyond memory. Although these models are often interpreted as focusing on the end product of hippocampally supported retrieval (i.e., of a scene or event), they both incorporate distinct views on the online processing requirements of mental construction (i.e., forming a scene vs. detail recombination for scene construction and constructive event simulation theories, respectively). Our framework complements both of these theories by holding mental construction as a central hippocampal function, and extends them by specifying the type of mental constructions required, particularly with respect to intrahippocampal functional organization (for related findings, see Ref. 137). By incorporating these distinctions, our framework harmonizes existing



**Figure 5.** Left: a depiction of the experimental design used by Sheldon and Levine<sup>107</sup> to test medial temporal lobe (MTL) contributions to different forms of naturalistic relational retrieval. There were three conditions. Each trial used a randomly selected pictured object (e.g., a teddy bear) to cue the requested information. In the event condition, participants were asked to use the object to think of a specific past personal event. In the within-item condition, participants were asked to generate and relate together concepts and features of the object. In the item-context condition, participants were asked to think of a specific location related to that object and relate other objects that would also be at that location. Right: the MTL patterns of activity extracted from a multivariate analysis. Red indicates areas that are recruited by autobiographical retrieval (the event condition). Green indicates areas that were recruited by the conceptually driven within-item condition. Blue indicates areas that were recruited by the perceptually driven item-context condition.

theoretical accounts of the hippocampus. This framework is consistent with the view that the hippocampus is fundamental for relating together all forms of information from memory<sup>20,21,132</sup> and posits that the hippocampus is specialized in processing particular types of information along the long axis.

As mentioned earlier, another prominent distinction in hippocampal processing concerns the underlying computations. David Marr’s landmark 1971 paper<sup>138</sup> set the stage for viewing the hippocampus as a structure that supports learning and memory via pattern-separation and pattern-completion mechanisms.<sup>35–38</sup> When learning, the hippocampus engages in pattern separation to encode events as unique, sparse representations by acting as an

index to details of memory that are stored in associated regions of the neocortex. When remembering, pattern-completion mechanisms use a portion of an event code or representation to reactivate the stored representation, reconstructing that memory, although separation, can also occur at retrieval (for a review, see Ref. 37). We speculate on how these mnemonic computations can be integrated for different types of mental construction, which we predict will be an emerging new trend in autobiographical memory research (also see Refs. 15 and 80).

Mental construction, as we have defined it in this paper, relies on the dynamic interaction of pattern separation and completion. We speculate that pattern separation is required to lay down a trace

for mental construction, particularly in open-ended scenarios. Pattern completion is required to reinstate event representations in order to retrieve multimodal details of previous experiences, either as a fully realized past event or as a series of partially formed representations to access details that can be used to create a novel mental construction. We integrate these ideas with models of hippocampal functional organization and expand on them below.

Anterior hippocampal–medial prefrontal cortex interactions are needed to integrate experiences into existing knowledge structures.<sup>139–141</sup> We suggest that these interactions also serve to revive similar events and their associated details. This information can be integrated into constructions in which the converging concept is a goal, via pattern-separation mechanisms. We further speculate that the posterior hippocampus will be recruited when mental construction is required at a finer level of perceptual resolution, either for existing schemas (i.e., well-defined retrieval that does not typically recruit the hippocampus) or goal-oriented constructions, including remembering. For these constructions, the converging concept is or becomes an image or internal percept; thus, pattern-completion mechanisms of the posterior hippocampus will be recruited to flush out (or complete) representations with additional details. The advent of new neuroimaging tools, particularly multivoxel pattern analysis, is well equipped to test these hypotheses.

In addition, there are now a number of innovative techniques that can be used to explore network differences, including multivariate analytic tools and functional connectivity analyses such as graphical theory analysis of network activity. Thus, while we have focused on the hippocampus, future research should explore how the dissociations proposed here are driven by hippocampal–cortical interactions, as already illustrated by studies of MTL networks that reflect functionally distinct anterior and posterior memory subsystems.<sup>142,143</sup>

In conclusion, our framework rests upon determining the commonalities that weave together autobiographical memory and other forms of retrieval to better understand hippocampal form and function (for a related view, see Ref. 94). While we do not claim to capture the entirety of hippocampal contributions to information learning and retrieval, we highlight when the hippocampus is most robustly involved in mental construction, providing pivotal

insights into adaptive cognitive functions. With our proposed framework, we anticipate new research into the benefits and limits of hippocampal contributions to detailed open-ended retrieval in the real world.<sup>144</sup>

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## Conflicts of interest

The authors declare no conflicts of interest.

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