

# Details, gist and schema: hippocampal–neocortical interactions underlying recent and remote episodic and spatial memory

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Memories are complex and dynamic, continuously transforming with time and experience. In this paper, we review evidence of the neural basis of memory transformation for events and environments with emphasis on the role of hippocampal–neocortical interactions. We argue that memory transformation from detail-rich representations to gist-like and schematic representation is accompanied by corresponding changes in their neural representations. These changes can be captured by a model based on functional differentiation along the long-axis of the hippocampus, and its functional connectivity to related posterior and anterior neocortical structures, especially the ventromedial prefrontal cortex (vmPFC). In particular, we propose that perceptually detailed, highly specific representations are mediated by the posterior hippocampus and neocortex, gist-like representations by the anterior hippocampus, and schematic representations by vmPFC. These representations can co-exist and the degree to which each is utilized is determined by its availability and by task demands.

## Addresses

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## Introduction

It is well established that the hippocampus is needed for the acquisition and retention of recently acquired spatial and episodic (or context-dependent) memory [1–3,4<sup>\*</sup>,5,6]. There is also a consensus that these types of memory are not stored in the hippocampus as such. The memory trace, or engram, consists of an integrated hippocampal–cortical

ensemble of neurons, with the hippocampus binding information and providing the sparsely distributed code ‘pointing to’ the cortical (and subcortical) neurons where information about the content and conscious experience of the memory is represented [7].

What is the nature of the sparse code that is represented in the hippocampus? Many alternatives have been proposed, leading to debates about the role of the hippocampus in consolidation [3,4<sup>\*</sup>,5,8–13] and the types of memories dependent on hippocampal function [1,2,14–20]. By one view, the hippocampus is a temporary memory structure that is implicated in retention and retrieval only until the identical memory is consolidated in extra-hippocampal structures in the neocortex [9,10,21]. An alternative view, provided by the Trace Transformation Theory, and the Multiple Trace Theory from which it is derived, is that the hippocampus continues to be implicated in retention and retrieval of perceptually-rich, detailed memories, in perpetuity [3,4<sup>\*</sup>,5,22]. This framework predicts that the specificity of a memory, namely its gist and perceptual features, remain hippocampally-dependent, but memories can also be transformed with time and experience to more schematic or semantic representations, which become independent of the hippocampus.

*Gist* refers to the central features of a particular episode (story line), and is distinct from *schema*, which refer to ‘adaptable associative networks of knowledge extracted over multiple similar experiences’ [23,24], capturing similarities *across* particular episodes. Thus, a gist representation may not be richly detailed but is still specific to a single episode (‘my tenth birthday party’), while a schema is a more abstract representation based on multiple similar episodes or memories (birthday parties in general). Crucially, schema, gist and detailed representations are not mutually exclusive. These differing representations may co-exist and support one another or may be preferentially retrieved at the expense of the other(s) based on the particular demands of a task. Thus, it is the quality or *nature* of the memory representation, rather than its age, that determines whether it is dependent on the hippocampus.

In this review we discuss primarily recent evidence supporting the hippocampus’s role in the representation of perceptually-rich memories including episodes and scenes, how some of these memories are transformed with time and experience, relinquishing their hippocampal

representation, and how this evidence informs theories of memory systems and hippocampal function (see [4,5,23–28] for previous reviews in humans and rodents). In the second section, we discuss evidence for functional differentiation along the long-axis of the hippocampus. In the third section, we propose how such differentiation relates to the questions above concerning the nature of hippocampal and neocortical memory representations. Throughout, we consider transformations to include forgetting of perceptual and contextual details, distortions, extraction of statistical regularities among instances, and assimilation to schemas while preserving the central elements (gist and schema) of the memory.

### The nature of episodic and spatial memory representations as revealed in studies on memory consolidation and transformation

Extensive hippocampal damage typically impairs memory for specific episodes no matter how long ago they were acquired [29,30], but more nuanced patterns of deficits are revealed in individuals with partial damage. Medial temporal lobe epilepsy (mTLE) that affects the hippocampus leads to autobiographical memory loss extending back to early childhood [31]. To investigate the nature of this loss, St-Laurent *et al.* [32] had people with mTLE and healthy controls retrieve detailed memories of remote autobiographical events and recently viewed video clips. The pattern of results was remarkably similar in both cases: patients' memory was relatively preserved for the gist, or story elements, of the event (i.e. those elements central to plot coherence), but their memory was clearly impaired in describing the perceptual details. A subsequent fMRI study indicated that hippocampal activity was reduced, but not absent, in mTLE patients, suggesting that the preserved gist elements may have been supported by some hippocampal activation [33]. Their impoverished memory for details was associated with reduced activation in posterior neocortex which is functionally connected to the posterior hippocampus (pHPC). In healthy young adults, memory conditions with richer perceptual details were associated with right hippocampal activation [33], providing additional evidence that the hippocampus supports richly detailed memories.

In a related study, Sekeres *et al.* [34] (see also [35]) showed, in healthy controls, that over the course of a week, memory of peripheral details (perceptual and contextual details that are not central to the plot) is diminished compared to memory for central details which capture the gist of the clip. Preliminary evidence shows that this pattern of forgetting is accompanied by diminished posterior hippocampal activation, relatively preserved anterior hippocampal activation, and increased vmPFC activation which suggests an increased reliance on gist and schematic information to compensate for the lack of available detail. The interaction among medial temporal and prefrontal

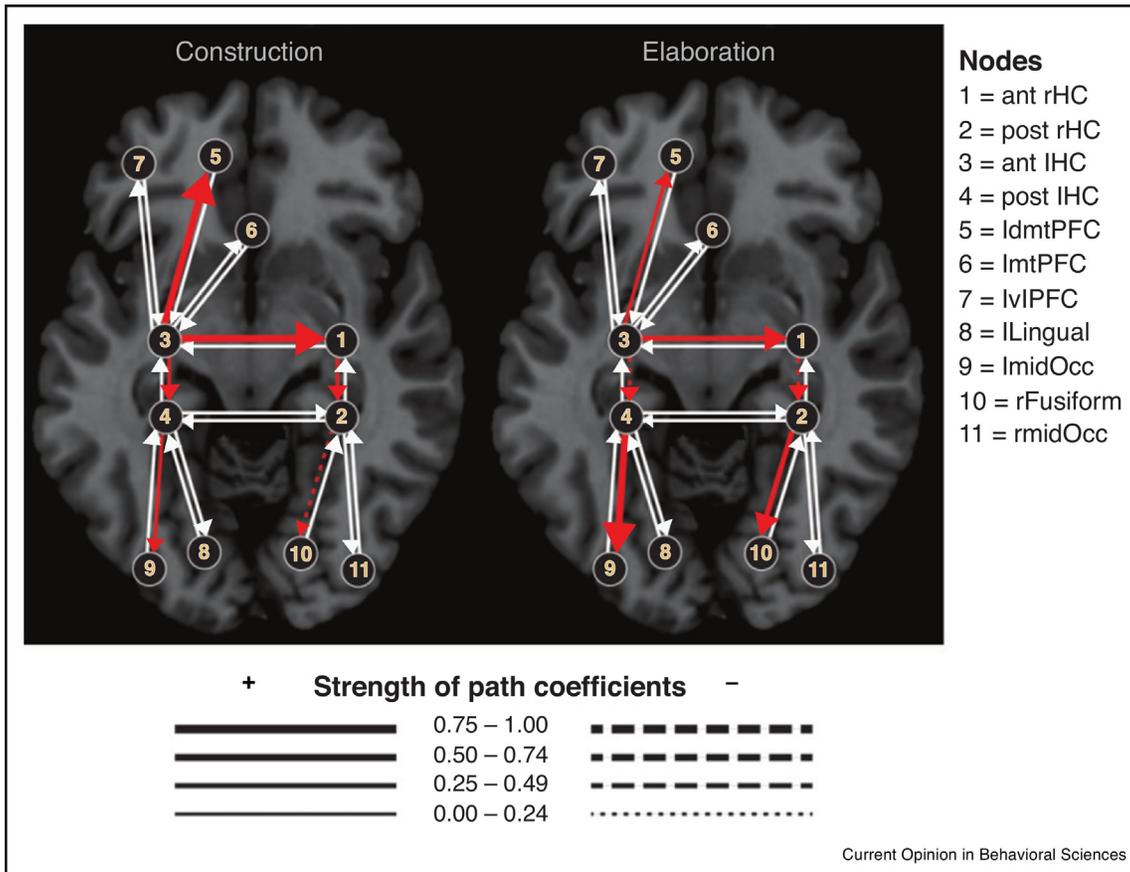
regions in retrieving autobiographical memory in healthy participants is depicted in Figure 1.

Similar patterns are observed in spatial memory. Patients with hippocampal lesions, though severely impaired in acquiring new spatial information, and in recovering detailed perceptual representations of locations incidental to navigation, retain the ability to navigate normally, and to perform well on tests of allocentric spatial memory in familiar environments, including on such demanding tests as vector mapping [36,37]. Likewise, former taxi drivers with degeneration or lesions of the medial temporal lobes (MTLs) can navigate along main roads that they have travelled many times, and form the core of their schematic representation, but lose the ability to travel on less central roads that require more detailed memory representations to navigate [38,39]. Similar patterns of loss of highly detailed spatial memory with retention of more general representations have been shown in ageing studies of both humans and rodents [40,41]. We interpret these data as showing that patients with hippocampal damage can retain and retrieve a schematic representation of a well-learned environment that is sufficient for navigation along major or highly familiar thoroughfares, but not the incidental perceptual or peripheral details that enable them to re-experience the environment.

These findings on patients have been corroborated in functional neuroimaging studies of healthy people. In a longitudinal study involving real-world navigation of routes in Toronto, Hirshhorn *et al.* [42] found that the hippocampus was recruited during navigation tasks when people had lived in Toronto for six months or less, but that hippocampal involvement in navigation was absent after they had lived there for a year, with greater involvement of neocortical regions including the inferior frontal gyrus, parahippocampal cortex and superior temporal cortex, possibly indicating that highly detailed representations were no longer needed to make such judgments. A subsequent study of individuals who had lived in Toronto for five years or more indicated that making precise, as compared to coarse, topographical discriminations uniquely recruited the right pHPC [43]. In a related behavioural study, comparing the performance of young adults with older adults, the two groups performed comparably on schematic tests of spatial memory, but the older adults were deficient in recognizing and re-experiencing vivid details from the environment [40]. In a subsequent study, Herdman *et al.* [37] showed that patients with MTL lesions were similarly impaired at describing detailed routes, but not in their schematic representations of routes.

Together, these studies demonstrate that for both spatial and episodic memory, highly-detailed representations or those that require great precision are perpetually dependent on the hippocampus, while more generalized,

Figure 1



Hippocampal–neocortical interactions during autobiographical memory retrieval. Healthy controls were required to retrieve an autobiographical memory in response to a cue ('First Kiss') and indicate when they had done so by pressing a key (Construction Phase). Having retrieved the memory, they then had to recover as much detail as possible about it (Elaboration Phase). As Figure 1 illustrates, functional connectivity between the aHPC and vmPFC is stronger during the construction phase, when the gist of the memory is constructed, and between the pHPC and posterior neocortex, during the detail elaboration phase [89]. Red arrows represent positive (solid) or negative (dashed) effective connections that differed between construction and elaboration phases, and the thickness of the arrows represents relative strength of the connections. White arrows depict connections that were included in the model but did not differ between construction and elaboration phases. Other studies have shown that in patients with mTLE, there is decreased hippocampal activity, and stronger connections between medial prefrontal and medial temporal and parietal cortical regions during autobiographical memory retrieval [90].

schematic representations can be supported by neocortical regions and survive hippocampal damage (but see [38]). For episodic memory, the vmPFC plays a prominent role. Pre-existing schemas mediated by the vmPFC, may be activated at encoding and re-activated at retrieval [44]. When the novelty of an event is such that pre-existing schemas are absent or weak, neocortical representations involving the vmPFC may strengthen over time as opportunities for repeated encoding, retrieval, and replay during sleep increase [45]. vmPFC representations, however, can co-exist with those in aHPC and pHPC, even at remote time points.

Consistent with this view, Bonnici *et al.* [46,47,48] have shown that over two years, representations of highly detailed memories in humans increase in the vmPFC

and pHPC, whereas representations in aHPC remain relatively stable. Increased pHPC involvement in remote memories may be required to maintain the same level of detail as in recent memories. Similar evidence of increased vmPFC involvement in remote memory comes from a host of studies in rodents [25]. In a recent study, Kitamura *et al.* used optogenetic techniques in transgenic mice to silence or activate neurons recruited during initial encoding of a contextual fear response [49]. They found that mPFC neurons were recruited, but not implicated, in contextual fear memory at initial learning when hippocampal cells were involved. As the memory aged, and hippocampal cells became silent, mPFC neurons matured and became viable mediators of the remote memory [49], though the absence of a hippocampal response suggests that the remote memory likely was less detailed [5,50].

According to our framework, damage or dysfunction that affects the entire hippocampus, but spares the vmPFC should lead to loss even of gist, and sparing of only general memories [27]. Few studies have addressed this possibility directly, but we note that HM [30,51], KC [52,53] and other severely impaired amnesics [54] have few, if any, memories of specific autobiographical events, only generic memories, and any memories of specific events are likely semanticized [27,55]. Conversely, damage to the vmPFC leads not only to impaired remote memory, and even recent memory, if schemas play a role in acquisition [56–58] or control [59], but in humans vmPFC damage is accompanied by confabulation, a disorder that arises from poor schema instantiation accompanied by poor monitoring and control [24,60,61].

For remote spatial memory, it is not clear whether schematic representations in the absence of the hippocampus depend on the vmPFC [62], or on other neocortical structures, such as the parahippocampal cortex, retrosplenial cortex and parietal regions involved in navigation [42,63]. In addition, while spatial memory appears to demonstrate the same pattern of loss of specific detail following hippocampal damage, it is not clear what the spatial equivalent of gist (the central details of a single event) might be, and if this is retained in cases of partial hippocampal damage that spares the aHPC (see [49]). In the next section, we describe differences along the hippocampal long-axis, which may further illustrate how the degree of detail of both spatial and episodic memories relates to their neural substrate.

### **Specialization along the longitudinal axis of the hippocampus: Gist and detailed representations mediated by anterior and posterior hippocampus**

As we noted, the type and specificity of memories may influence activity levels along the long-axis of the hippocampus during memory encoding and retrieval, based on anterior–posterior differences in functional neural organization, such as receptive field size, the distribution of hippocampal subfields, and their connections to other brain regions [4,64,65]. Recent evidence suggests that in humans, as in rodents [66], the pHPC represents more fine-grained, local (spatial) features of the environment, which underlie detailed, perceptually-based memory representations [67–69]. The representations mediated by pHPC likely relate to its strong connectivity with regions in posterior neocortex that process perceptual and spatial information such as ventral temporal cortex, precuneus, retrosplenial cortex and posterior cingulate cortex [70,71]. By comparison, the aHPC, with strong connectivity to the anterior temporal lobe and medial prefrontal cortex, associated with semantic memory and schema, respectively [70,71], represents coarser, more global representations and relations which support the gist of an episode or an environment (see [59,72,73] for related proposals).

Several studies of spatial memory that require learning the positions of objects in space have found that more coarse-grained spatial representations such as the identity of the context, or large-scale spatial relationships recruit the aHPC while fine-grained spatial relationships including the relative positions of items in an environment recruit pHPC [67–69]. These distinctions among different levels of spatial representation seem to align with the topological structure of an urban environment, with the pHPC tracking local topology (degree centrality; the number of available path options to the present street), the anterior hippocampus global topology (closeness centrality; how close one street is to others in the overall network), and no hippocampal activation for betweenness centrality (how frequently a street is traversed to get from one street to another) which characterizes major thoroughfares [74\*]. Importantly, these studies highlight that spatial memories are not exclusively dependent on aHPC or pHPC, but that the locus of activity varies based on the scale of detail required for the particular memory task.

An elegant study by Collin and colleagues replicated these effects for event memory, finding evidence for the representation of small-scale event networks in the pHPC and more general, large-scale networks in the aHPC [75\*]. A related study found that learning a connection between two previously unrelated events led to increased similarity of activity for those events in mPFC and pHPC, suggesting that gaining schematic knowledge about events may reconfigure activity patterns in mPFC and the hippocampus [76]. A meta-analysis by Viard *et al.* [77] noted that the pHPC is implicated in re-experiencing the past, which entails the retrieval of detailed perceptual and information associated with the event, and in the episodic events with the greatest detail. Likewise, personal cues, of the sort associated with gist information, activated the anterior hippocampus. Last, in older adults (over 55), whose ability to re-experience the past in great detail is compromised relative to younger adults, activity is greater in the anterior hippocampus, consistent with their greater reliance on gist [77]. Evidence from animal research also corroborates these views, suggesting that the dorsal HPC (equivalent to the human pHPC) represents aspects of events in more fine-grained detail than the ventral HPC (equivalent to the human aHPC), and that the prefrontally-mediated schemas interact with the hippocampus to guide behaviour [78–82].

Recent studies suggesting a specialized role for the aHPC (and the anterior subiculum, in particular) in scene construction [83,84,85\*,86,87] may appear to be inconsistent with this view, since scenes are often rich in detail. We underline, however, that scenes, like episodes, can vary in their detail-richness, based on the contents of memory or particular task demands. In many cases, a scene may be represented in a gist-like manner, which would still entail a specific spatial representation but without elaborating

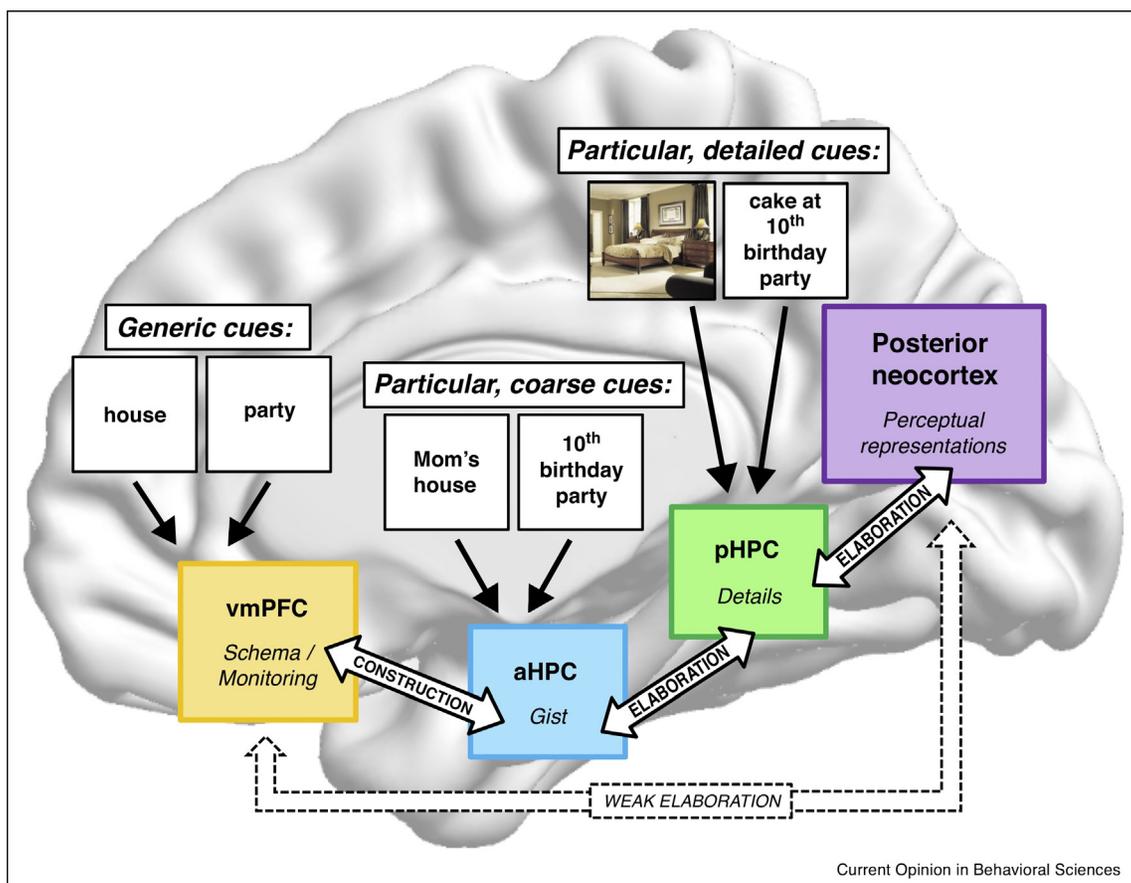
many details, even if they are available. For example, even if there is access to a very detailed mental image of 'Mom's house', only a less elaborated gist-like representation may be used in accord with task demands, and therefore, pHPC will not be engaged. Consistent with this interpretation, in two studies by Zeidman and colleagues [83,85<sup>\*</sup>], aHPC was commonly activated across various scene tasks, with pHPC activation occurring in conditions that likely involved the most detailed representations. In one study [83] perceiving a visual scene, in which fine-grained details are provided by the stimulus, led to activity throughout the aHPC and pHPC while mentally imagining a scene only recruited aHPC. In a second study [85<sup>\*</sup>], where vividness was explicitly measured, the most vividly recalled scenes were those that engaged the pHPC. A recent study by Gaesser *et al.* [88] is also consistent with this interpretation. They found that

constructing rich, imaginary scenarios for the first time engaged the pHPC compared to re-constructing already imagined scenarios, suggesting that events may be elaborated in less detail after repeated retrieval.

### Interactions of aHPC, pHPC and vmPFC in support of spatial and episodic memory representations varying in detail

Thus, we suggest that differences in the detail-richness of scenes and episodes lead to differential recruitment of the aHPC and pHPC. Differential involvement of the aHPC and pHPC, as well as their connectivity to neocortical structures, such as posterior neocortex and vmPFC, may help, therefore, to better characterize the representations associated with spatial and episodic memory, and their interactions during retrieval of recent and remote memory (see Figure 2 for illustration). With a general or coarse

Figure 2



Schematic of the representations mediated by hippocampal and ventromedial prefrontal cortical regions, and their interactions. Activations of the vmPFC, aHPC and pHPC, and the interactions among them, are influenced by the nature of the information the structures help represent, the type of cues used to elicit memories, and the goals of the memory task. Thus, generic cues will preferentially engage the vmPFC, particular cues at a coarse level of detail, the aHPC and particular cues at a fine level of detail, the pHPC. In response to generic or particular cues, the initial phases of memory retrieval involve memory construction, which implicates interactions between vmPFC and aHPC, likely via the middle layer of entorhinal cortex [111]. Later phases in which the memory is fleshed out with details, involve a process of elaboration that recruits pHPC and interactions with posterior neocortex, including parietal and occipital regions involved in perceptual representations. If the cue is highly detailed, the pHPC may be engaged directly via a process of pattern completion. If the hippocampus is damaged, or memory is highly schematic, the vmPFC and posterior neocortical regions may interact directly to generate a less detailed representation.

cue, the early phases of memory retrieval will often involve construction process, mediated by the aHPC and vmPFC, while later phases will involve detail elaboration, recruiting the pHPC and posterior neocortical regions [89]. More specific cues leading directly to detailed representations may entail earlier pHPC activity. In cases of hippocampal damage, the vmPFC may interact with posterior neocortical regions more directly, but the memories retrieved would lack specificity and detail-richness [90,91] (see [Box 1](#) for a possible framework for this flexible connectivity). Similarly, particular emphasis on perceptual details will preferentially recruit the pHPC and posterior neocortex, whereas reliance on coarser representations will differentially engage the aHPC and vmPFC. Thus, if memories are transformed with age and lose detail, their representation will shift from the pHPC towards aHPC and vmPFC. If detail is preserved, pHPC representation will be maintained (or even increased, see [46\*,48]), while vmPFC representations are also formed.

Although this proposal is consistent with data reviewed above on the performance and patterns of neural activation in studies of recent and remote memory in healthy controls and individuals with MTL lesions, many aspects of this proposal require further study, particularly experiments designed to measure or control the specificity and detail of memories. Would a specific memory low in detail still recruit the aHPC in absence of pHPC activation? What types of coarse-grained spatial memories can be retained after partial hippocampal damage? Do general or specific cues differentially affect activity and its timecourse along the hippocampal long-axis [92\*]? In addition, questions remain about how long-axis differentiation is realized in hippocampal subfields, and if certain subfields are specialized for spatial or non-spatial representations [84,86,87,93–95]. Although we

have focused primarily on loss of details with time and experience, it is important to know whether the model can also account for other forms of memory transformation [96]. Last, while we have limited our review largely to the hippocampus and vmPFC, interactions and connectivity with areas throughout the medial temporal lobe and autobiographical memory network will be crucial in understanding how memories are represented over time. Namely, how the proposed functions of the aHPC and pHPC relate to closely interconnected neocortical areas including the perirhinal and parahippocampal cortices.

## Conclusion

We have reviewed evidence that the hippocampus is involved in long-term memory for detailed representations episodic and spatial memory (for possible behavioural consequences of this shared dependence, see [Box 2](#)). A challenge for future research is in differentiating among schematic, gist-like and detailed representations in both spatial and episodic memory and linking them specifically to the neural regions proposed. In keeping with the nomenclature proposed in our paper, we acknowledge that this proposal is currently more of a schematic or gist-like representation of the literature, and awaits detailed elaboration at both the neural and functional level. Work along these lines, employing high resolution neuroimaging, multivariate and time frequency analyses has already begun (e.g. [85\*,97,98]). We anticipate that future studies that probe the nature of spatial and episodic memories along the long-axis, its subregions and their interactions with related structures, will be able to address questions of memory representation and dynamics in more detail and precision.

### Box 1 Memory networks and process specific assemblies.

The hippocampus is part of a larger autobiographical memory/recollection/spatial memory network that includes parahippocampal cortex, retrosplenial cortex, anterior cingulate, inferior parietal cortex, and vmPFC. One research strategy has been to determine how the regions of the network are co-activated during memory encoding and retrieval. As shown in McCormick *et al.*'s study on functional connectivity ([Figure 1](#)), different components of the network are engaged during different phases of autobiographical memory retrieval. Cabeza *et al.* [4\*,99,100] have proposed that small networks, which they termed process specific assemblies (PSA), are assembled to mediate a specific cognitive operation, which rapidly disassemble when the operation is no longer needed. Different regions of the hippocampus interacting with anterior and posterior neocortex constitute such PSAs. Given that PSAs are rapidly assembled and disassembled, they require a mechanism that can quickly control communication between distant brain regions. Recent research suggests that neural oscillations are a likely candidate mechanism supporting rapid PSA dynamics [4\*,101,102].

### Box 2 Interactions between spatial and episodic memory.

How do the similarities between the neural correlates of spatial and episodic memory relate to their interactions in behaviour? A number of studies of episodic memory and imagination have found that events in more familiar contexts are more detailed and vivid than those in less or unfamiliar contexts [103–108]. In a recent study, we found that even if no spatial context were specified when imagining an episode, individuals spontaneously assigned familiar contexts to the events, and these events were remembered in more detail and more vividly than those without spatial contextual information [106]. The primacy of spatial context was also evident in its efficacy and superiority as a cue for episodic memory compared to more thematic cues [92\*] and its tendency to be remembered first and leading to more rapid retrieval when recalling autobiographical memories [109]. These studies suggest that spatial context may support more detailed and vivid episodic memory, and provide more rapid access to them, perhaps due to a stronger spatial scaffold on which the memories are formed. These findings are consistent with Scene Construction Theory [14–16,27,84,87], as well as with Event Memory Theory [110], which propose a central role for scenes in binding event information in memory and imagination.

## Conflict of interest statement

Nothing declared.

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