Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in
Behavioral Sciences

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

Jessica Robin[1,2] and Morris Moscovitch[1,2]

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
[1] Psychology Department, University of Toronto, 100 St. George Street, Toronto, ON M6S 3G3, Canada
[2] Rotman Research Institute, Baycrest Health Sciences, 3560 Bathurst Street, Toronto, ON M6A 2E1, Canada

Corresponding author: Moscovitch, Morris (momos@psych.utoronto.ca)

Current Opinion in Behavioral Sciences 2017, **17**:114–123

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

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

http://dx.doi.org/10.1016/j.cobeha.2017.07.016

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•,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’ 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•,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•,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,