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Episodic Memory and Beyond: The Hippocampus and Neocortex in Transformation

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Annu. Rev. Psychol. 2016. 67:105–34

The *Annual Review of Psychology* is online at psych.annualreviews.org

This article's doi:
10.1146/annurev-psych-113011-143733

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Keywords

episodic memory, frontal cortex, hippocampus, parietal cortex, schema, transformation

Abstract

The last decade has seen dramatic technological and conceptual changes in research on episodic memory and the brain. New technologies, and increased use of more naturalistic observations, have enabled investigators to delve deeply into the structures that mediate episodic memory, particularly the hippocampus, and to track functional and structural interactions among brain regions that support it. Conceptually, episodic memory is increasingly being viewed as subject to lifelong transformations that are reflected in the neural substrates that mediate it. In keeping with this dynamic perspective, research on episodic memory (and the hippocampus) has infiltrated domains, from perception to language and from empathy to problem solving, that were once considered outside its boundaries. Using the component process model as a framework, and focusing on the hippocampus, its subfields, and specialization along its longitudinal axis, along with its interaction with other brain regions, we consider these new developments and their implications for the organization of episodic memory and its contribution to functions in other domains.

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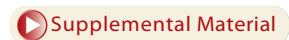
INTRODUCTION

The concept of episodic memory, according to Tulving (1983, 2002), refers to a declarative memory that contains information specific to the time and place of acquisition (what laypeople may call an autobiographical episode), as distinguished from semantic memory, which is concerned with knowledge not tied to its context of acquisition. Recollection, a process that enables one to relive episodes, is associated with autonoetic consciousness, a subjective sense of time and of the self as the one who experienced the episode and possesses the memory. By contrast, the process of knowing enables one to recognize an event or stimulus as familiar without locating it in time and place. Familiarity-based memory is associated with noetic consciousness, or at least with a much reduced autonoetic consciousness. Because these events and processes are what researchers studying episodic memory mean to capture in a laboratory setting, Tulving referred to the single,

unrelated trials that are the typical memoranda of laboratory experiments as events (or mini-events) embedded within the larger episode of the laboratory experiment. For an event to qualify as an episodic memory, details of the event and of the place in which it occurred must be present at retrieval, accompanied by autoegetic consciousness that enables reexperiencing [James 1950 (1890), p. 658; Tulving 1983, 2002; see Rubin & Umanath 2015 for a critique and alternative].

Tulving's formulation still governs much of the research on episodic memory and the brain, but the introduction of new topics, modes of inquiry, more naturalistic approaches and technologies has added great variety to the landscape. It is this altered landscape that we wish to capture in our review. Because it is considered central to our understanding of the brain basis of episodic memory, the hippocampus (HPC) serves as the hub of our article, much as it is considered the hub of regions dealing with episodic memory. The article focuses on four parts: (a) the role the HPC plays in representing the various aspects and attributes of episodic memory; (b) other structures that are implicated in different aspects of episodic memory and its transformation to gist and semantics; (c) the contribution of the HPC and episodic memory to nonepisodic memory functions such as priming, short-term memory (STM), and semantics and to nonmnemonic functions such as perception, problem solving, decision making, and language; and finally, and briefly, (d) the functional and structural connectivity between the HPC and other regions and networks implicated in episodic memory.

In the interest of space and timeliness, we favored the most recent references and reviews over early empirical papers. All figures accompanying the review can be downloaded by following the **Supplemental Material link** in the online version of this article or at the Annual Reviews home page at <http://www.annualreviews.org/>. We regret that owing to space limitations we could not cover in detail, and sometimes not at all, many topics relevant to episodic memory, such as emotion, reward, individual differences, and lifespan development.



COMPONENT PROCESSES AND DYNAMIC HIERARCHIES

We use a component process model as our framework. Building on Tulving's ideas, and the acknowledged role of the HPC in memory, Moscovitch & Winocur (1992; also Moscovitch 1992) proposed that at encoding the HPC obligatorily binds together into a memory trace or engram (Dudai 2012, Josselyn et al. 2015, Tonegawa et al. 2015) those neural elements in the medial temporal lobe (MTL) and neocortex that give rise to the multimodal, multidomain representations that constitute the content of a conscious experience. The experience includes the accompanying phenomenological awareness and reflects a process involving the network interactions that make up the experience itself (Moscovitch 1995). In this view, consciousness, or the phenomenology of experience, is inextricably linked to episodic memory. The episodic memory trace or engram consists of a bound ensemble of HPC-neocortical neurons with a sparsely coded HPC component. This is envisioned as a spatial scaffold or matrix (Nadel 2008, O'Keefe & Nadel 1978) that acts as a pointer or index (Teyler & Rudy 2007) to neocortical components that together represent the totality of the experience, including not only the perceptual, emotional, and conceptual details that form the content of the experience, but also the processes that imbue it with a sense of autoegetic consciousness. Because HPC binding is obligatory, storage is random, and only close temporal contiguity, or close contiguity with a reinstated context, determines the elements that are bound to each other.

At retrieval, the HPC-neocortical ensemble is reactivated in a two-stage recollection process by an internal or external cue. The first involves a rapid and unconscious interaction between the cue and HPC (ecphory), which in turn reactivates the neocortical traces bound with it. The process may end here or proceed to the second stage. In the second stage, which is slower and conscious,

cortical processes operate on the output of the first stage to reinstate the conscious experience of the episode (Moscovitch 2008). Because the HPC-mediated operations, once initiated, are obligatory, control processes at encoding and retrieval, mediated by prefrontal cortex (PFC) and related structures, operate on the information delivered to the HPC and on the output from it to make memory intelligent and goal directed.

Hippocampus, Neocortical Connections, and Specialization Along Its Long Axis

The HPC sits at the top of a hierarchy of largely cortical systems (the ventral and dorsal streams) in which later stages integrate information from previous ones, building more complex representations in the process and influencing the operation of earlier stages through back projections (Nadel & Peterson 2013) [**Supplemental Figure 1** (follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>)].

Receiving its input from the entorhinal cortex, which in turn receives its input from the perirhinal cortex (PRC) and the parahippocampal cortex (PHC), the HPC integrates information about complex object representations from the PRC and view-specific scene representations from the PHC into a view-invariant representation that “frames the spatial relations among the various parts of the environment” (Nadel & Peterson 2013, p. 1248) and locates those parts and their features within that spatial frame (Bird & Burgess 2008, Hassabis & Maguire 2009, Nadel 2008). HPC-mediated memories are said to reflect relational associations (Eichenbaum et al. 2007, Olsen et al. 2012), in that both the separate elements of some event and their relation retain their distinctiveness.

This framework focuses primarily on representational inputs to the HPC from the posterior neocortex, and it says nothing about HPC connections to anterior structures such as the amygdala (emotion), anterior temporal cortex (semantics), and PFC [schemas and working memory (WM)]. These structures play different, but important, roles in episodic memory through their interaction with the HPC. We will pay some attention below to the relation of the HPC to the ventromedial PFC (vmPFC). Readers interested in the interactions between HPC and lateral frontal cortex during encoding and retrieval should refer to Simons & Spiers (2003) and Anderson & Huddleston (2012), and to Talmi (2013) on amygdala and emotion.

The HPC creates the same kind of representation throughout its length, but at different scales. At the posterior end, its representations capture detailed information about local spatiotemporal aspects of an experienced event based on input from the posterior neocortex. At the anterior end, its representations capture global aspects of an event (i.e., the general context and the emotion and meaning attached to it) based also on interactions with the anterior neocortex. Thus, these two types of HPC representation arise primarily from differences in input-output connections along the long axis of the HPC (Poppenk et al. 2013, Strange et al. 2014) [**Supplemental Figure 2** (follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>)]. This framework sets the stage for investigating the contribution of various HPC subfields to episodic memory (see below) and for understanding how memories are transformed from detailed representations to schematic ones at both functional and neurological levels (Penfield & Mathieson 1974).

Memory Transformation

As Bartlett (1932) noted, memory representations are not static entities but change throughout an individual’s life with time and experience. As we discuss in the sections that follow, some memories retain their highly detailed specificity and, as the data suggest, continue to rely on the

HPC and remain recollective; others are transformed through forgetting or schematization, so that they lose details and retain only the gist or familiarity; and others become incorporated into a semantic network and acquire its properties. The latter cases rely more on neocortical structures, with the vmPFC and anterior temporal lobe prominent among them. In some cases, specific and gist-like representations can coexist, leading to dynamic interactions and to the dominance of one memory over the other or to the conversion of one type to the other, depending on circumstances. The neural instantiation of these memories corresponds to their functional representation, in accordance with what we believe is a general principle in cognitive neuroscience: Representations that differ from one another must necessarily be mediated by different structures (collections of neurons), and representations mediated by different structures must necessarily differ in some fundamental way from one another. This principle, which we call functional-neural isomorphism (F-NI), helps account for patterns of HPC-neocortical involvement during memory consolidation.

Process-Specific Alliances

Not all components of the HPC nor of the neocortical (and other) structures with which they interact are activated at the same time or in all tasks. Instead, we conceive of subsets of components forming temporary process-specific alliances (PSAs) whose composition is determined by the moment-to-moment demands of a task. Whereas the posterior neocortical components, in conjunction with the posterior hippocampus (pHPC), determine the local, spatio-perceptual aspects of the experience, anterior components of the HPC, in conjunction with the anterior temporal lobe, PFC, and amygdala, represent conceptual and emotional aspects. The PSAs also include control structures that regulate encoding and retrieval. All these memory components can interact with components earlier and later in the hierarchy, and in other domains, such as language, planning, and decision making, leading to the involvement of the HPC, and by inference episodic memory, in nonmnemonic functions (see below).

The updated component process model makes the following assumptions:

1. During perception, sensory information is progressively bound into feature clusters in early sensory regions, into integrated objects and contexts in late sensory and cortical MTL regions, and into complex events binding objects with their spatiotemporal contexts together with the feeling (phenomenology) of experience in the HPC.
2. The same regions remain active for a while due to top-down modulation from the PFC, which allows the persistence of object and context representations, as well as unified event representations, within WM.
3. During encoding, a fraction of transient representations in WM are transformed to a long-lasting format in the cortex and HPC. The HPC representation points to the location of cortical memory traces (HPC-cortex PSA). This encoding process is supported by schematic relational processes in the vmPFC [aHPC-vmPFC PSA; anterior hippocampus (aHPC)] and semantic processes in the ventrolateral PFC (vlPFC) (vlPFC-MTL PSA) and anterior temporal cortex.
4. Finally, during retrieval, access to the integrated event representation in HPC leads to the reactivation of the MTL and posterior cortices, hence to cortical memory traces (HPC-cortex PSA) (stage 1) and to the awareness of the recovered memories, involving regions such as the ventral parietal cortex (VPC) (HPC-VPC PSA) (stage 2). As in the case of encoding processes, these retrieval processes are supported by control processes mediated by the PFC. Oscillatory mechanisms are assumed to contribute to all these four groups of processes.

PERCEPTUAL (LOCAL) DETAILS AND EVENT (GLOBAL) ELEMENTS

Episodic Details and Representations

It is generally agreed that patients with extensive bilateral damage manifest a global anterograde amnesia that affects acquisition, retention, and retrieval of all episodic memories. This includes the particular details of the event as well as its theme and general structure, though it is the episodic details that are most severely affected. When damage is more restricted, confined to small portions of the HPC, or unilateral, the relative sparing of acquisition of gist and semantic memory compared to episodic memory is more noticeable (Winocur & Moscovitch 2011, Winocur et al. 2010).

To measure these aspects of autobiographical memory retrieval, Levine et al. (2002) created the Autobiographical Interview (AI), whose scoring distinguishes between different internal details that are unique to the event (perception, emotions, locations) and capture episodic aspects of it, and external details, which are not unique to the event and capture more semantic aspects. Administering the AI to patients with unilateral temporal lobe epilepsy or lobectomy that included the HPC, St-Laurent et al. (2014) found that memory for perceptual details was most affected; memory for more global details, such as the story elements that comprise the series of events within an episode, was also impaired, but not as severely; and memory for external details was preserved. Using the AI, or a variety of similar tests such as the Autobiographical Memory Inventory (Kopelman et al. 1989) and the Test Episodique de Mémoire du Passé autobiographique (TEMPau) task (Piolino et al. 2009), investigators found the same pattern of impaired episodic but relatively spared semantic aspects of autobiographical memory in patients with MTL lesions or dysfunction, regardless of etiology (transient epilepsy, ischemic attacks, degenerative disorders such as Alzheimer's disease, amnesic variant of minimal cognitive impairment, later stages of frontotemporal dementia, and psychiatric and mood disorders; reviewed in Piolino et al. 2009, Viard et al. 2012, Winocur & Moscovitch 2011).

In functional magnetic resonance imaging (fMRI) studies of autobiographical memory, HPC activation has been shown to be modulated by the number of details or the vividness of the recalled autobiographical event, which is correlated with internal details (Sheldon & Levine 2013; reviewed in Cabeza & St. Jacques 2007, Svoboda et al. 2006, Winocur & Moscovitch 2011). It is noteworthy that HPC sensitivity to details and vividness was also observed when recollecting generic and often repeated events such as family dinners (Addis et al. 2004); this is consistent with findings from patients and suggests a general HPC propensity for representing details (Rosenbaum et al. 2009, Rubin & Umanath 2015).

Film clips provide more experimental control than tests of autobiographical memory, yet they retain a naturalistic quality. The pattern of results obtained with clips in patients with MTL lesions (St-Laurent et al. 2014), compared to HPC activation in healthy controls in fMRI studies, was similar to that obtained on recall of autobiographical episodes (Ben-Yakov & Dudai 2011, Furman et al. 2012, Maguire & Mullally 2013) [**Supplemental Figure 3** (follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>)].

Although the use of more naturalistic stimuli has grown, by far the largest majority of studies use unrelated stimuli as the method of choice in studying episodic memory, sometimes presented in arbitrary contexts and tested almost exclusively by recognition. It is reassuring, therefore, that similar regions are activated when laboratory memory studies emphasize recollection (but not familiarity), whether measured subjectively, by asking individuals to rate the extent to which the item evoked the experience at study (recollection or know response), or objectively, by asking individuals to recognize elements of the context in which the stimulus appeared (source memory) (Skinner & Fernandes 2007). Known as the recollective network, these regions overlap

substantially with those activated during recall of vivid, autobiographical memories (Cabeza & St. Jacques 2007, Rugg & Vilberg 2013, Svoboda et al. 2006) and include HPC, PHC, medial prefrontal cortex (mPFC), VPC (angular gyrus), and retrosplenial cortex/posterior cingulate [**Supplemental Figure 4** (follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>)]. As with more naturalistic tests, the degree of HPC activation is associated with the amount of detail that is retrieved (Rugg & Vilberg 2013) or its contextual specificity (Cohn et al. 2009, Sadeh et al. 2012), but not with memory strength, even when great care is taken to equate recollection and familiarity with strength (Migo et al. 2012, Montaldi & Mayes 2011; but see Squire & Wixted 2011).

With respect to performance in patients with MTL lesions that include the HPC, Montaldi & Mayes (2011) and Yonelinas (2013) concluded that even when overall accuracy, an index of strength, is equated, memory under conditions associated with recollection is selectively impaired compared to memory based on familiarity (for counterarguments, see Dede et al. 2013, Squire & Wixted 2011). By contrast, familiarity-based memory is impaired and recollection is preserved following PRC lesions that spare the HPC (Bowles et al. 2010).

As we noted earlier, recollection, mediated by the HPC, depends on relational yet flexible associations among disparate (random) and distinct (separable) elements (for reviews, see Eichenbaum et al. 2007, Olsen et al. 2012, Yonelinas 2013). When associations lose their relational nature and become unitized (e.g., combining the words fire and dog into fire-dog), HPC involvement as inferred from lesion (Quamme et al. 2007) and fMRI (Haskins et al. 2008) is diminished or lost.

Spatial Details and Representations

Because all autobiographical events unfold in a particular spatial context, it has been argued that spatial context has a privileged status in episodic memory, consistent with the HPC's role in spatial memory and navigation (Buzsaki & Moser 2013, Nadel 2008). The scene construction hypothesis holds that the HPC is necessary for constructing coherent scenes that provide the scaffold or framework for supporting memory for events (Hassabis & Maguire 2009). Studies of patients with HPC lesions and functional neuroimaging studies in healthy people show that constructing coherent scenes is dependent on the HPC (Maguire & Mullally 2013). Moreover, there is great overlap among brain regions and networks activated on spatial tasks and on episodic memory tasks, even when the latter do not have an obvious spatial component (Spreng et al. 2009). Robin et al. (2015), however, found that even when narratives lack information about spatial location, participants spontaneously add them at encoding or recall, which may account for some of the overlap.

There is evidence that memory for events is facilitated by familiar spatial information (e.g., Robin & Moscovitch 2014), and that regions sensitive to memory for events interact with regions sensitive to spatial memory in the HPC even at the single-cell level (Miller et al. 2013). In a study that suggests the primacy of spatial over event memory in the HPC, Chadwick et al. (2010) had participants recall in detail film clips in which two different events occurred in two distinct spatial locations. Using multivariate pattern analysis (MVPA) to differentiate neurally the retrieved memories from one another, they found that classification accuracy for distinct episodes was significantly better than chance only in the HPC. When required to classify the clips with regard to differences in location as compared to event content, only locations could be classified accurately, and then only in the HPC.

Temporal Details and Representations

Time is a central aspect of episodic memory. Events unfold in time just as they unfold in space. However, evidence for a hippocampal role in forming, maintaining, and retrieving temporal

associations, as well as relating them to events, is controversial: Some consider time to be a derived property, whereas others consider temporal coding to be a core function or property of the HPC (Dalla Barba & La Corte 2013, Davachi & Dubrow 2015, Eichenbaum 2014, Howard & Eichenbaum 2013).

There are at least three aspects of temporal processing that have been addressed in the literature (Schacter et al. 2012): (*a*) the temporal tag or signal associated with different moments in the unfolding of an event, which can also code for duration; (*b*) the coding for the temporal order of elements within and across episodes; and (*c*) the subjective sense of time, so that we can identify our experience of the memory as occurring in the near or distant past or future.

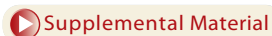
To account for the first two aspects, based on evidence from time cells (Eichenbaum 2014), investigators have proposed a hippocampal mechanism that could construct a scale-invariant representation of time over hundreds of seconds; this could serve as the contextual/neuronal background in which events are embedded via association (Howard & Eichenbaum 2013). This model can account both for temporal order effects in memory and for the reduction in temporal precision with temporal distance. Davachi & Dubrow (2015) noted that contiguity as a determinant of temporal order is better for elements within an event or segment than across them, pointing to an important role for event segmentation. They also note that learning a sequence through repeated presentations may rely on pattern completion, with one item serving as a cue for eliciting replay of the associated elements. Although both proposals are broadly consistent with the temporal contiguity aspects of the component process model, it remains to be explained why, in general, memory for temporal information is very poor in comparison to memory for spatial information.

Memory for duration and temporal order across very short intervals such as milliseconds, and across long intervals such as minutes, hours, or days, seems to depend on information and strategies mediated by extrahippocampal structures (Davachi & Dubrow 2015, Moscovitch 1992), among them the cerebellum, PFC, posterior parietal cortex (PPC) (Danckert et al. 2007), and basal ganglia. The cognitive processes and neural mechanisms that underlie our subjective sense of time as past, present, or future are even less well understood, though some have proposed that the HPC plays a crucial role. The growing interest in the temporal aspects of memory will hopefully stimulate research that will add to our meager knowledge of them and resolve some of the controversies.

INTRAHIPPOCAMPAL SPECIALIZATION

Memory Precision, Pattern Separation, and Hippocampus Subfields

Although there is ample evidence that relational associations account for our ability to recollect the details of an episode, a number of studies suggest that the precision, or high resolution, of those memories is a critical component even for recognition of single items such as faces, as long as the items are complex and the targets are distinguished from similar lures after a long delay (Craik 1986, Smith et al. 2014a, Yonelinas 2013). To account for this sensitivity to complexity and precision, investigators have pointed to a fundamental computational mechanism, called orthogonalization, instantiated in the organization and operation of the projections between two hippocampal subfields, the dentate gyrus (DG) and CA3. This orthogonalization, or pattern separation that is dependent on DG, yields distinct representations that enable memory precision between items (or collections of items) with overlapping features (Hunsaker & Kesner 2013, Norman 2010) [Supplemental Figure 5 (follow the Supplemental Material link in the online version of this article or at <http://www.annualreviews.org/>)]. The efficiency of pattern separation



should determine the precision of the memory and the number of separable details held in memory (Poppenk et al. 2013).

Recent advances in high-resolution fMRI have allowed investigators to test these ideas more directly. Bakker et al. (2008) found that DG/CA3 (which were considered together because they could not be delineated separately) showed the greatest sensitivity to tests of memory discrimination between highly similar items (which they presumed depended on pattern separation). CA1, on the other hand, showed a linear response and tracked the similarity matrix, indicating that the more similar the items were, the more likely they were to be coded as the same. Pattern separation was related to recollection (Kim & Yassa 2013) in younger adults. Older adults showed a reduction in DG/CA3 responsivity to pattern separation but normal CA1 responses, consistent with their poorer ability to distinguish targets from similar foils at recognition (Yassa et al. 2011). Importantly, the extent of HPC involvement in distinguishing between target and lures may depend on whether the differences between them are relational or based on single features (Aly et al. 2013, Yonelinas 2013).


The same involvement of HPC subfields is evident in distinguishing among more naturalistic stimuli. Precision of episodic recall of film clips, as measured by the extent to which participants could rate the clips as different, was related to the size and activity of the CA3 region (Chadwick et al. 2014) [**Supplemental Figure 6** (follow the **Supplemental Material** link in the online version of this article or at <http://www.annualreviews.org/>)]. Comparable findings were reported by Bonnici et al. (2013) for autobiographical memories in the pHPC, where remote, but not recent, memories could be distinguished from one another only in DG and CA3.

By contrast, CA1 is presumed to collate information generated through pattern completion in CA3 and to deliver it back to the entorhinal cortex after having compared it with the current perceptual input. CA1, therefore, can act as a match-mismatch detector and facilitate the laying down of new memories and retrieval of old ones (Ben-Yakov et al. 2014). Selective damage to CA1, therefore, leads to extensive episodic memory loss (Bartsch et al. 2011, Zola-Morgan et al. 1986).

SPECIALIZATION ALONG THE LONGITUDINAL AXIS OF THE HIPPOCAMPUS

The distribution of the hippocampal subfields is not uniform along the longitudinal axis (Malykhin et al. 2010). DG/CA3 ratios are higher in the pHPC than in the aHPC, with greater CA1 proliferation in the anterior portion. This would suggest more powerful pattern separation capabilities in the pHPC than in the aHPC, a notion that fits well with recent work demonstrating greater precision and detail in the grain of HPC representations and reduced receptive field size of place cells as one moves from anterior to posterior regions (Strange et al. 2014). Neuroanatomical (Aggleton 2012) and connectivity analysis during resting state (Ranganath & Ritchey 2012) showed that the pHPC is preferentially connected to perceptual regions in the posterior neocortex, whereas the aHPC is preferentially connected to anterior regions, such as the vmPFC and the lateral temporal cortex extending into the temporal pole and the amygdala, which are associated with the processing of schemas, semantic information, and social and emotional cues, respectively. These connectivity patterns could conspire to create unique aHPC and pHPC encoding and representational environments, with the aHPC coding information in terms of the general or global relations among entities, and the pHPC coding information in terms of precise positions within some continuous dimension (Poppenk et al. 2013) (**Supplemental Figure 2**).

The evidence generally supports the model (see Poppenk et al. 2013 for review). Whether on tests of autobiographical memory (Nadel et al. 2013) or on laboratory tests of spatial memory

 Supplemental Material

(Evensmoen et al. 2015), aHPC activity is associated with the general locations where events occurred or coarse map-like representations of those locations, whereas activity in the pHPC is associated with local details or finer-grained maps (for comparable results in rodents see review in Preston & Eichenbaum 2013). Similar effects are found in studies of real-world navigation in a virtual environment. Greater aHPC activation is associated with increased distance between sequentially presented landmarks (Morgan et al. 2011), greater scale of the environment (Baumann & Mattingley 2013), and direction to goal, whereas pHPC activations are inversely correlated with distance to goal (Howard et al. 2014). Consistent with this model, and with the hypothesis that recollection is associated with memory for local details, Poppenk & Moscovitch (2011) found that individual differences in recollection were correlated with the size of the pHPC (and the pHPC/aHPC ratio), which in turn was related to the functional connectivity of the pHPC with posterior neocortical regions at rest.

With respect to autobiographical memory, our framework has much in common with Conway's (2009) nested hierarchical model, in which a conceptual frame provides contextualizing knowledge that helps locate and organize the local perceptual and spatial details that comprise the episode [Supplemental Figure 7 (follow the Supplemental Material link in the online version of this article or at <http://www.annualreviews.org/>)]. Retrieving the frame of the episode or the lifetime period in which it occurred, which is a typical first step in constructing memory for an autobiographical episode, is often associated with aHPC and neocortical activation, whereas recovering and elaborating the perceptual details of the event is associated with pHPC activation (McCormick et al. 2013, St-Laurent et al. 2014; for review and other evidence, see Schacter et al. 2012).

Such differences are also observed when considering global and local aspects of a single object. The neural suppression that occurs when an object is repeated is seen in the DG/CA3 subfields of the aHPC, but when fine discrimination between targets and similar lures is required, then the pHPC is activated (Reagh et al. 2014).

Similarly, encoding novel events, or forming relational associations between random items, is associated with aHPC activation, possibly because such activities typically involve higher-order conceptual processing, whereas encoding familiar or repeated events relies less on such conceptual processes and more on attending to perceptual aspects of the event (Poppenk et al. 2013). Since repeated events also have a retrieval component, this formulation is consistent with evidence of differential aHPC and pHPC activation at encoding and retrieval (Kim 2015).

The global-local hypothesis of anterior-posterior HPC organization that we propose provides a plausible first approximation of functional organization along the long axis of the HPC with respect to episodic memory. Another virtue of this conception of aHPC function is that it serves as a bridge between detailed episodic representations that are dependent on the HPC and more schematic, gist-like representations that emerge as memories are transformed with time and experience (Preston & Eichenbaum 2013, Robin et al. 2015, Winocur & Moscovitch 2011) and become reliant on extrahippocampal structures, such as the vmPFC and anterior temporal lobe, that have strong aHPC connections.

MEMORY CONSOLIDATION, TRANSFORMATION, AND ASSIMILATION

Postencoding Consolidation

Episodic memory is dynamic, with significant transformations occurring throughout the memory's lifetime (Bartlett 1932, Dudai 2012). In accord with our model, and with the principle of F-NI,

these transformations are accompanied by corresponding shifts in underlying neural structures that support different kinds of memory representations.

Studies of postencoding consolidation indicate that different processes are predictive of better memory for the studied material, such as a spike in HPC activity immediately after the end of an event (Ben-Yakov & Dudai 2011), event-specific reactivation of encoding processes during rest (Staresina et al. 2013), and increased connectivity between the HPC and structures specialized in processing associated stimuli measured at rest after a block of associative memory study trials (Tambini et al. 2010). Memory can be reduced by interference from other stimuli (Ben-Yakov et al. 2013) or enhanced by emotional stimuli (Dunsmoor et al. 2015) presented during this postencoding period.

Postencoding processes during sleep have complex effects on memories acquired during the previous day, and recent work suggests that their impact may be related to the type of memory examined as well as to the stages of sleep under study (Diekelman & Born 2010, Stickgold 2013). With respect to episodic memory, there is evidence that recollection can be preserved or degraded and transformed to familiarity, but the conditions that lead to one or the other outcome, and the neural mechanisms involved, have yet to be elucidated (Lewis & Durrant 2011).

Remote Memory

The issue of memory transformation lies at the heart of the debate on the neural representation of remote memory, in which changes can occur across weeks, years, and even decades (Nadel & Moscovitch 1997, Winocur & Moscovitch 2011). The observation that remote, compared to recent, memories appear to be relatively spared following damage to the MTL, and the HPC in particular, formed the foundation of the standard consolidation theory (SCT). This theory states that the HPC serves as a temporary memory structure needed only until memories are consolidated elsewhere, presumably in the neocortex, where they are retained and from where they can be retrieved. Although Penfield & Milner (1958) and Penfield & Mathieson (1974) noted that extra-HPC memories are generalized (gist-like) and fundamentally different from the detailed, specific memories mediated by the HPC, some versions of SCT did not make any distinction between the two types of memory. In other versions, all remote memories were assumed to be incorporated into a neocortical semantic or schematic network, leaving no HPC-mediated specific episodic memories behind (Frankland & Bontempi 2005, McClelland et al. 1995, Wang & Morris 2010).

Drawing on the work of previous investigators, Nadel & Moscovitch (1997) took issue with each of these interpretations and with evidence that all remote memories are spared following HPC damage. They noted that individuals can retain detailed remote episodic memories and that the HPC and related structures are needed for their retention and retrieval, no matter how old the memories are. Reactivation of old memories leads to the re-encoding and formation of a rich distributed network of multiple traces in the HPC, which provides some protection from small, but not large, HPC lesions. Gist-like (semanticized) memories of episodes as well as semantic memories, mediated as they are by other structures, would survive HPC damage under any circumstances. The multiple trace theory proposed by Nadel & Moscovitch (1997) links the type of memory representation (detailed versus gist-like/schematic/semantic) with the structure that mediates it (HPC versus neocortex), and it helps account for the different patterns of retrograde amnesia observed after HPC damage.

Building on ideas from multiple trace theory, Winocur & Moscovitch (2011; see also Winocur et al. 2010) proposed that some autobiographical and spatial memories in humans, as well as context-dependent memories in rodents, are transformed with time and experience from highly detailed, context-specific memories to less detailed, schematic memories that retain the gist of

an experience or event or schematic representation of an environment, but not many particulars. These transformed memories are based on representations in extra-HPC structures and do not depend on the HPC. Insofar as memories remain detailed and retain their contextual specificity, they will continue to depend on representations encoded in the HPC, regardless of their age. Both types of representations can coexist and dynamically interact, so that a memory that has previously been manifested in a schematic rather than detailed form can regain its specificity with appropriate reminders and once again engage the HPC (Winocur et al. 2010, Winocur & Moscovitch 2011).

Appealing to the principle of F-NI, Winocur & Moscovitch (2011) reasoned that a memory that was once mediated by the HPC and is now mediated by the cortex must differ in accord with the processing and representational capabilities of these two structures. If the intricate architecture of the HPC is needed to perform the computations that are central to the retention and retrieval of precise, detailed, and relational representations of recent memories, it is difficult to see how comparable representations, only older, could be mediated solely by the neocortex, which lacks the requisite architecture.

The debate between adherents of each camp has continued for 20 years and has been reviewed extensively, so it will only be summarized here. Performance on tests of autobiographical memory that are especially sensitive to attributes that capture the essence of episodic memory—such as perceptual details, viewpoint specificity, vividness, judgments of recollection, and relational associations—suffers after HPC damage or dysfunction, regardless of etiology and of the amount of time passed since the memory was acquired. Unless the damage extends to extra-HPC regions, memories for gist or semantic aspects of personal experiences, public events, and well-known narratives such as bible stories and fairy tales are relatively well preserved (Winocur & Moscovitch 2011), though memory for details, even for well-known stories, may be compromised (Kwan et al. 2013, Verfaellie et al. 2014). The same is true of spatial memory: Memory for perceptual details needed to reexperience the environment (scene construction) is lost, whereas schematic memories sufficient for navigation are retained (Winocur & Moscovitch 2011).

Evidence from fMRI is consistent with this observation. Autobiographical memories that are detailed and vivid engage the HPC no matter how long ago they were acquired (Winocur & Moscovitch 2011). Importantly, the pattern of activation along the long axis of the HPC resembles that observed for recently acquired novel and familiar memories: More recent memories engage the aHPC and more remote ones engage the pHPC, and the distinction between recent and remote memories, and among the memories themselves, is mediated by the posterior DG/CA3 subfield (Bonnici et al. 2013). Likewise, connectivity of the HPC to other structures in the autobiographical memory network varies with vividness and remoteness (Furman et al. 2012, Sheldon & Levine 2013).

The same pattern of decreasing HPC and increasing neocortical activation with remoteness and accompanying loss of specificity or recollection is found in traditional laboratory tests of episodic memory with delays of one (Ritchey et al. 2015) to six weeks (Viskontas et al. 2009a; but see Nieuwenhuis & Takashima 2011 for different types of associative memories that may be schema dependent). Likewise, for remote spatial memory, studies suggest that what is preserved after HPC damage is a gist-like, schematic representation of the environment (essentially a coarse-grained map) that is adequate for navigation but not for conjuring up the kind of details that allow for reexperiencing the environment (Rosenbaum et al. 2000, Winocur & Moscovitch 2011). Consistent with this interpretation, HPC activation is found during mental navigation in a recently encountered environment but is diminished or absent when navigating in a familiar environment (Hirshhorn et al. 2012).

Proponents of the SCT argue that extensive retrograde amnesia for autobiographical events occurs only when lesions of the MTL extend beyond the HPC to include the temporal neocortex

(Squire & Wixted 2011). Although this explanation may account for deficits in remote memory in some patients, it cannot account for deficits in many others whose lesions are restricted to the HPC or its projections via the fornix (see review in Winocur & Moscovitch 2011), or to disruption restricted to CA1 fields in transient global amnesia (Bartsch et al. 2011). To account for fMRI results, proponents of the SCT have argued that HPC activity observed while recalling remote memories is related to the re-encoding of autobiographical memories retrieved from the neocortex rather than to the memories themselves (Squire & Wixted 2011). This critique is difficult to refute, though recent evidence of the different patterns of activation for recent and remote memories in the HPC and midline structures would argue against a simple re-encoding interpretation (Bonnici et al. 2013).

Recent and Remote Memory and Memory Transformation in Rodents

The most unequivocal evidence comes from studies of context-dependent (episodic) and context-independent (gist-like) memory in rodents, where considerable control can be exerted over the learning environment and over lesion location and extent. These data favor the transformation hypothesis. Longitudinal studies show a loss of contextual specificity of memories tested a month after acquisition compared to tests given shortly after learning (Winocur et al. 2010). This loss of context specificity is accompanied by a lesser dependence on the HPC and a higher dependence on the anterior cingulate cortex (ACC) or prelimbic cortex, the rodent homologue of the vmPFC in humans, as determined by both the effects of lesions and early gene expression (Frankland & Bontempi 2005, Winocur et al. 2010). Importantly, providing reminder cues in the long-delay condition a day prior to the test (Winocur et al. 2010) or periodically reactivating the context (de Oliveira Alvares et al. 2012) restore or maintain contextual specificity, rendering the memory once again HPC dependent and vulnerable to the effects of HPC lesions.

These findings provide a possible interpretation of system reconsolidation, a process whereby memories that once were believed to be consolidated in extra-HPC structures become labile once they are reactivated by a reminder (retrieval cue) and become vulnerable once again to the disruptive effects of HPC lesions, protein synthesis inhibitors, or synaptic interference (Dudai 2012, Nader & Hardt 2009, Wang & Morris 2010).

The fact that specificity and hippocampal dependence could be restored by reminders not only speaks to the dynamic nature of memory and against the SCT, but also suggests that some vestige of the original specific memory must be retained by the HPC. Evidence in support of this hypothesis comes from optogenetic studies in which temporary disruption of those CA1 cells that encoded the information leads to loss of contextual fear memories even at long delays (Goshen et al. 2011, Tanaka et al. 2014), just as CA1 disruption causes remote memory loss in humans (Bartsch et al. 2011). Recent studies in which cells that constitute the memory (engram) are labeled (tagged), reactivated, or suppressed support our hypothesis that long-term retention of context-dependent memories is mediated by neural ensembles in the HPC (Josselyn et al. 2015, Tonegawa et al. 2015).

Memory Transformation and the Ventromedial Prefrontal Cortex: Remote Memory and Schemas

The vmPFC seems to play a special role in mediating remote memories (Frankland & Bontempi 2005), but its precise nature is not clear. One promising clue to vmPFC function comes from the work of Tse, Morris, and collaborators (Tse et al. 2007; see Wang & Morris 2010) on schemas, which can be defined as “adaptable associative networks of knowledge extracted over multiple similar experiences” (Ghosh et al. 2014, p. 12057). Tse et al. (2007) showed that the vmPFC is

crucial for assimilating new olfactory-location associations into a spatial schema, which is acquired over many exposures. As a result, the new associations become independent of the HPC more quickly, relying instead on the ACC/vmPFC.

Such results are interpreted according to a schema modification model (Dudai 2012, Wang & Morris 2010), which posits that schemas provide the organizing structures that influence memory formation and retrieval (Bartlett 1932) as well as interpretation of ongoing events. We propose that the vmPFC, with its reciprocal connections to the aHPC, could act as a hub binding the global context of events represented in the aHPC and general knowledge, including that about the self, into a schema that captures what is common to all such events (see also Benoit et al. 2014). A fundamental function of any schema is to make predictions about what one should expect to experience in a given context/situation/setting, to aid in interpreting events that occur there, and to enable one to notice new details that do not fit the schema. For example, one may have schemas of what kitchens are like and what one does in them. Walking into a strange kitchen may produce a novel episodic memory for the kitchen and for the local events that transpire there; schemas ensure that the experience of being in the kitchen is not in itself strange but relatively predictable.

Some investigators have suggested that the vmPFC is the consolidated (remote) memory homologue of the HPC, taking over its function. This notion runs counter to the F-NI principle. Our proposal is that the vmPFC and HPC may both deal with context, but of fundamentally different sorts. The HPC binds together local and global contextual information about a specific event or environment, whereas the vmPFC binds together what is common across similar events and possibly helps “decide” which among them is relevant for a particular task (Preston & Eichenbaum 2013).

A number of predictions follow from this hypothesis:

1. Insofar as retrieval is dependent on the vmPFC without HPC involvement, the retrieved memory will be gist-like or general, rather than detailed and specific. This appears to be the case in humans and rodents with HPC damage.
2. The vmPFC should interact with the aHPC to encode schematic information and to help retrieve detailed information via schema-related cues (for similar proposals, see Conway 2009, Preston & Eichenbaum 2013, van Kesteren et al. 2012). The vmPFC’s role in retrieval becomes more prominent as local perceptual details mediated by the pHPC are degraded, making retrieval more dependent on the global aspects of the memory represented in the aHPC (Bonnici et al. 2013, Sheldon et al. 2013).
3. Damage to the vmPFC, therefore, should be more evident in tests of remote, rather than recent, memory, and vary inversely with the specificity of retrieval cues.
4. The vmPFC may be implicated more as structured events are transformed or when isolated events are experienced within a structured context, as in Tse et al.’s (2007) studies and Takashima et al.’s (2009) human analogue of them, but not when events are isolated and random as in many traditional laboratory experiments.
5. Following vmPFC damage, schema formation and representation may itself be impaired, so that what delineates a schema (e.g., what one does in a kitchen) is distorted, nebulous, or overinclusive (Ghosh et al. 2014). Consequently, individuals with vmPFC damage may experience the present, and reexperience the past, through the lens of distorted or misapplied schemas, and this may contribute to confabulation, a memory disorder characterized by the production of patently false information about autobiographical episodes, personal semantics, historical events, and common narratives (Gilboa & Verfaellie 2010, Moscovitch & Winocur, 2002, Schnider 2008, Shallice & Cooper 2012).

Interim Summary

Memories for recent events draw on interactions between schemas, semantics, and perceptual aspects of an experience, mediated in part by different regions in the anterior and posterior neo-cortex. These are bound together in relational representations mediated by the pHPC for local details and the aHPC for global context, accounting for the specificity characteristic of episodic memory (Craik 1986). Over time, detailed information about local aspects of the event become degraded or lost, and our memory reports come to rely on more global aspects mediated by the aHPC in conjunction with schema-related information mediated by the vmPFC. The latter helps determine performance when the HPC is entirely lost. Damage to the vmPFC leads to deficient and distorted use of schemas in memory, perception, and reasoning.

CONSCIOUSNESS, THE HIPPOCAMPUS, AND THE LATERAL AND POSTERIOR PARIETAL CORTEX

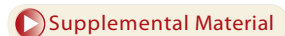
Consciousness is a defining feature of episodic memory, as evidenced by the fact that performance on a variety of implicit or nondeclarative tests can be normal in patients with MTL damage and severe episodic memory deficits (Moscovitch et al. 1993). These findings suggest the following conclusions: (a) The HPC, and by implication recollection, does not contribute to normal performance on nonepisodic memory tasks such as priming; (b) the HPC can only process consciously apprehended information; and (c) consciousness invariably accompanies the retrieval of the detailed information that underlies recollection. In the last decade, each of these conclusions has been challenged and effectively overturned.

The two-stage model of recollection predicts that priming for relational associations should be preserved insofar as it draws on information underlying the first rapid, nonconscious stage of recollection mediated by the HPC. Recent studies show that priming of relational associations, measured by manual reaction times (Schacter et al. 2004) or eye movements (Hannula & Ranganath 2009), is accompanied by HPC activation, is impaired in people with HPC damage (Olsen et al. 2012), and is more robust for items that are subsequently judged to be recollected than for familiar ones (Sheldon & Moscovitch 2010). Going one step further, Henke and collaborators showed that the HPC encodes information presented subliminally as long as it is relational (Henke 2010).

The Ventral Posterior Parietal Cortex and Subjective Aspects of Memory (Autooetic Consciousness)

Consistent with our component process model, studies on nonconscious memory suggest that engagement of the HPC is not sufficient for explicit recollection or episodic memory, and that other structures also need to be recruited. Structures in the frontoparietal network are among the possible candidates. Here we focus on the PPC, since it has been the object of much debate concerning its role in episodic memory.

Activation of the PPC, particularly on the left, often accompanies memory retrieval on laboratory tests of recognition and autobiographical memory (Cabeza & St. Jacques 2007, Rugg & Vilberg 2013, Svoboda et al. 2006). Of the two major divisions of the PPC, dorsal parietal cortex (DPC) and VPC, the VPC is associated with successful recollection, source monitoring, and high-confidence responses, whereas the DPC is associated with familiarity and low-confidence responses (for other differences between the two divisions, see Cabeza et al. 2012) [Supplemental Figure 8 (follow the Supplemental Material link in the online version of this article or at <http://www.annualreviews.org/>)].



A number of hypotheses have been proposed to account for VPC involvement in episodic memory, and recent reviews have discussed extensively their merits and deficiencies (Berryhill 2012, Cabeza et al. 2012, Rugg & Vilberg 2013). Here, we focus on the hypothesis that the VPC is implicated in the apprehension of the subjective qualities of memory (Simons et al. 2010). This hypothesis accounts not only for the reduced and less detailed recollections of patients with VPC lesions that can be ameliorated by cuing (Berryhill 2012, Davidson et al. 2008), but also for the low confidence the patients have in their memory even when source accuracy is high (Hower et al. 2014, Simons et al. 2010), an outcome that can be produced in normal people by deactivating the VPC with theta burst stimulation (Yazar et al. 2014). These findings raise the possibility that the VPC, perhaps via its interactions with the frontal cortex, is an essential component for enabling auto-noetic consciousness. It is interesting in this regard that VPC activation accompanies memories that come to mind involuntarily, either when they are elicited by a cue (Hall et al. 2014) or when they overcome active suppression (Benoit et al. 2014). It is also noteworthy that the VPC has been associated with functions that are the hallmarks of auto-noetic consciousness: WM and attention, time perception, feelings of intentionality, and a sense of self associated with theory of mind (ToM) (see Berryhill 2012, Cabeza et al. 2012). As noted, the VPC is also linked with the PFC (Prebble et al. 2013), another region that is associated with ToM (Mitchell 2009) and whose damage, or disconnection, can lead to reduced recollection and deactivation of the VPC (Levine et al. 2009).

These findings suggest a dissociation between successful retrieval of the content of episodic memories and the phenomenological experience that accompanies successful retrieval. It remains to be determined whether the diminished auto-noetic consciousness associated with VPC and PFC damage or disconnection results from an impaired postretrieval process that, as part of the second stage of recollection, attributes phenomenological experience to a detailed memory, or whether it results from loss of the “consciousness feature” of the HPC-neocortical engram, which VPC codes much as inferior temporal structures code for perceptual features.

BREAKING DOWN BORDERS AND CONQUERING DOMAINS

Following the introduction of the concept of episodic memory in 1972, much research has focused on how to distinguish episodic memory from other cognitive functions in general, and in particular from other forms of memory, at both the functional and neural levels. Given the widespread connections of the HPC (Aggleton 2012, Ranganath & Ritchey 2012) and its position in the component process model, the isolation and encapsulation of episodic memory could not be sustained. The last decade has seen an imperialist encroachment of episodic memory and the HPC into various domains, from perception to imagination, and from decision making to food regulation (Robinson et al. 2013, Rozin et al. 1998). We highlight four of these domains and consider how they relate to our model (see also Rubin et al. 2014).

The Hippocampus, Perception, and Working Memory

The idea that the HPC sits at the end of a perceptual hierarchy, receiving input from lower levels and projecting back to them, suggests that HPC influence should be felt in perception and WM, thereby eroding the hard and fast distinction between long-term memory (LTM), perception, and WM. According to the hierarchical representation model (HRM; Lee et al. 2012), the HPC’s role at the top of the hierarchy and the role of the structures below it are defined strictly not in terms of memory or perception, but rather (or also) in terms of the representations they support, consistent with the component process model. Insofar as the HPC represents relational information among separable entities, or even among features in single complex stimuli, perceptual discrimination

based on such features activates the HPC and is impaired in people with HPC damage (Lee et al. 2012, Yonelinas 2013).

Drawing on their theory stating that the HPC is implicated in scene construction, Mullally et al. (2012) showed that boundary extension—the normal tendency to reconstruct a scene with a larger background than actually was presented—was markedly diminished in patients with HPC lesions compared to controls, even when stimuli were presented as briefly as 200 ms [**Supplemental Figure 9** (follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>)]. In subsequent neuroimaging studies, Chadwick et al. (2013) showed that boundary extension is accompanied by hippocampal activation that, in turn, projects down the hierarchy to levels in the visual cortex.


HPC has also been shown to be implicated in STM and WM, especially if precision and relational binding are required (Olsen et al. 2012, Yonelinas 2013). Binding errors in reporting information in STM in people with HPC damage (Pertzov et al. 2013) and matching a target array of items on a screen with a test array presented shortly afterward was shown to be associated with HPC activation and to be reduced in people with medial temporal/HPC damage (Nichols et al. 2006, Olson et al. 2006; but see Talmi et al. 2005) or atrophy; the reduction was correlated with the extent of posterior hippocampal atrophy for location and with perirhinal atrophy for objects (Das et al. 2015). Performance on all the tests was correlated with estimates of recollection, whereas only performance on the object test was correlated with familiarity.

Though such developments blur the boundaries between LTM, WM, and perception, obliterating them would obscure the striking differences one sees clinically: Patients with HPC lesions rarely complain of perceptual or WM deficits but always complain of episodic memory deficits, whereas the reverse is true of people with damage to levels that are lower in the hierarchy. Capitalizing on this observation, Squire and collaborators (e.g., Kim et al. 2015, Squire & Wixted 2011) presented evidence showing that if the lesions were confined to the HPC and the tests did not implicate LTM, then perception and STM/WM was normal in patients with HPC lesions (see also Baddeley et al. 2010 and rebuttal in Clark & Maguire 2016; Maguire et al. 2015).

To counter this negative evidence, and the arguments based on it, Yonelinas (2013) and Lee et al. (2012) have argued, in accord with the HRM, that the complexity of the items and the precision of the discrimination determine HPC involvement on tests of perception and STM/WM. Moreover, it is likely that susceptibility to interference increases as one moves up the hierarchy, and hence the impact on memory is more keenly felt when higher levels are damaged. The component process model and the F-NI principle are consistent with either account, and the resolution of the debate rests on the question of whether HPC-mediated relational processing applies only to memory or also to perception (see also Clark & Maguire 2016, Maguire et al. 2015).

Episodic Simulation, Problem Solving, Empathy, and Decision Making

One of the most striking findings in recent years points to the large overlap in processes and structures involved in retrieving episodic memories, imagining future personal events, and constructing scenes, thereby propelling the HPC into domains it had not occupied previously (Addis & Schacter 2011, Buckner 2010, Maguire & Mullally 2013, Schacter et al. 2012, Viard et al. 2012). Because HPC-based memories are relational, their elements could be recombined to form new associations, which together with constructive processes dependent on the pHPC (Gaesser et al. 2013) would create new scenarios (Romero & Moscovitch 2012) and construct new scenes (Hassabis & Maguire 2009) in the service of current needs. Addis, Schacter, and colleagues referred to this as episodic simulation, a cognitive operation that draws on processes similar to episodic memory to create imagined events [see Maguire & Mullally (2013), who argue that scene construction is the fundamental process].

 Supplemental Material

Recent studies have shown that episodic simulation can lead to better social problem solving (Sheldon et al. 2011), greater empathy (Ciaramelli et al. 2013), and more willingness to help people in distress (Gaesser & Schacter 2014); in all cases, performance was related to the vividness or level of detail of the simulation. HPC damage or deterioration with aging leads to a drop in problem-solving performance (Sheldon et al. 2011) and reduces empathy in general (Beadle et al. 2013, Davidson et al. 2012), whereas training on recovery of episodic details improves problem solving (Madore & Schacter 2014). On the other side of the coin, vivid negative images associated with past events and conjured spontaneously in social situations contribute to social anxiety (Moscovitch et al. 2013).

Episodic simulation also influences decision making, as illustrated on tests of temporal discounting (i.e., the tendency to discount rewards if they are delayed). Benoit et al. (2011) showed that temporal discounting can be reduced by imagining in detail how one would spend the money in the future as compared to merely thinking conceptually about its usefulness; the extent of the reduction is related to vmPFC activation and its functional connectivity with the HPC. Consistent with the fMRI results, Palombo et al. (2015) showed that episodic simulation is ineffective in reducing the normal tendency for temporal discounting in people with amnesia associated with MTL damage (Kwan et al. 2013), because their capacity for simulation is compromised.

Whereas episodic simulation depends on conscious processes, unconscious stage-one associative processes mediated by the HPC likely underlie performance on tests of associative inference. In such tests, participants are shown overlapping pairs of items (e.g., AB and BC) and learn to associate A with C though they never co-occur. Shohamy & Wagner (2008) showed that this effect is mediated by the HPC and occurs at encoding without the participant's awareness, such that when BC is presented, the common element, B, reactivates the previously learned association, AB, and integrates both with C, a process they termed integrative encoding. This accords with the principle of obligatory binding of elements occurring in close temporal contiguity. Similar processes influence reward-based decisions in which a stimulus (A) acquires value through its secondary association (B) with monetary reward (C) (Wimmer & Shohamy 2012). The degree to which A comes to be associated with C is determined also by its interaction with schema-related processes in the vmPFC and its intrinsic resting-state connectivity with the HPC (Gerraty et al. 2014). Similar processes may underlie performance on tests of second-order conditioning in rats (Gilboa et al. 2014) and transitive inference in rats and humans who are presented with overlapping stimulus pairs in which one member of the pair is rewarded (e.g., $A > B$, $B > C$, $C > D$) and participants must infer how it is related to the other items (Preston & Eichenbaum 2013). If the latter task is solved by forming relational associations, then the HPC is necessary, but if it is solved by unitization, then it can be performed without recourse to the HPC but may still be dependent on the vmPFC and PRC (Ryan et al. 2013).

Such effects cannot be said to be related to full-blown episodic memory, which is defined as being associated with autoegetic consciousness, but should rather be related to operations of pattern separation, pattern completion, and associative binding that operate outside of conscious awareness but presumably underlie both episodic memory and these types of associative learning, in accord with the two-stage model of recollection and HPC activation. Consistent with this observation, Reber & Henke (2012) showed that associative inference based on integrative encoding can be attained even when AB and BC items are presented subliminally.

Language and Semantic Memory

Language processing was considered to be preserved in amnesia, at least as far as core phonological, syntactic, and semantic aspects were concerned (Corkin 2013). By and large, this view has not

changed, though it is fair to say that it has not been thoroughly explored either. However, in accord with the principle of F-NI, language and semantic memory should be no different than any other function if they draw on processes and representations mediated by the HPC. These are most evident in pragmatic uses of language, particularly in complex social discourse, which requires such HPC-mediated processes as the “flexible use of relational memory representations dredged from the past, and inserted appropriately into the flow of speech, or created rapidly in the present and incorporated effortlessly into the context that forms the common ground of social discourse” (Duff & Brown-Schmidt 2012). Discourse analysis reveals that such functions are aberrant or impoverished in amnesic patients (Race et al. 2015). The paucity of the experiential aspects of episodic memory in patients with HPC damage is revealed in their greater than normal selection of the definite over indefinite article and the diminished use of the historical present, a figure of speech in which a past event is referred in the present tense (e.g., Yesterday, I saw a fire; the fireman *goes* into the house, *battles* the flames. . .) and whose frequency of usage is correlated with the number of internal details in their narrative (Park et al. 2011).

As with language, insofar as semantic memory is informed by detailed, precise information about autobiographical events and allocentric spatial representations, it will be influenced by episodic memory representations mediated by the HPC. Evidence from studies of patients with amnesia and with semantic dementia suggests that people, places, public events, and even common objects and their names can be imbued with autobiographical significance (AS) in the sense that they automatically (either with or without conscious awareness) conjure up recollective information that facilitates naming, recognition, and semantic judgments. Consistent with the component process model, this AS advantage is lost in people with MTL damage (for review, see Renoult et al. 2012).

Renoult et al. (2015) used event-related potentials to explore this phenomenon further. When names of famous and nonfamous people were presented to participants in a nonepisodic fame-judgment task, they found that the amplitude of the N400 varied with the amount of the semantic, but not episodic, knowledge participants had about the people, whereas the reverse was true for the late positive component over the parietal electrode, which is sensitive to recollection.

These sets of findings suggest a novel interpretation of reports by Quiroga and collaborators (see review in Quiroga 2012), who found that single cells in the human HPC, which they named concept cells, respond selectively and invariantly to representations of famous people across modalities. Viskontas et al. (2009b), however, noted that the majority of the cells respond to people who are personally familiar to the patient. As in studies on AS, the pictures or names presented to the patients may automatically have evoked a recollective process, and therefore referring to the cells as AS or episodic cells would be equally appropriate.

The contribution of HPC-mediated episodic memory processes is also evident in tests of semantic fluency. Impaired performance on tests of semantic fluency following temporal lobe lesions has been shown to be related to HPC damage and not exclusively to lateral temporal damage as was once believed (Greenberg et al. 2009). This interpretation is supported by recent evidence from fMRI showing that HPC activation is associated specifically with the generation of episodic information from which semantic exemplars are derived, presumably by imagining personal experiences (e.g., evoking one’s kitchen if required to name kitchen utensils) when the most common exemplars are exhausted (Sheldon & Moscovitch 2012). Similarly, in a free association task to single words, responses become more idiosyncratic presumably because they are derived from personal episodic memories, whereas in patients with MTL lesions, the responses are fewer and less idiosyncratic because they rely more on semantic memory (Sheldon et al. 2013). Consistent with this finding is a report by Addis et al. (2015) showing

that performance on tests of divergent thinking is related to one's ability to construct episodic simulations and can be enhanced by inducing episodic specificity (Madore et al. 2015).

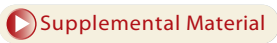
Although previously acquired semantic memory, stripped of episodic aspects, can be relatively spared in HPC patients, the acquisition of new vocabulary, though possible without the HPC, is laborious and poor (see Corkin 2013), but only if it depends on forming explicit relational associations between the target item and its name. Acquisition is relatively preserved, however, through fast mapping, an indirect associative procedure in which the participant discovers (infers) the association between the item and its name (Sharon et al. 2011). This fast mapping process may depend on rapid assimilation of the item to pre-existing schemas or semantic memory networks mediated by neocortex (Coutanche & Thompson-Schill 2015, Sharon et al. 2011). Item-name associations learned through fast mapping, however, are prone to catastrophic interference (Merhav et al. 2014). The reverse pattern, of better acquisition through the explicit route and poor fast mapping, is seen in patients with anterior temporal lesions that include the perirhinal cortex (Merhav et al. 2015, Sharon et al. 2011), suggesting that this structure may help mediate fast mapping. Not all attempts to replicate these fast-mapping results, however, have been successful (e.g., Smith et al. 2014b). The reasons for the discrepancies will need to be elucidated if we are to gain a better understanding of the neural mechanisms mediating fast mapping (Coutanche & Thompson-Schill 2015).

The evidence we reviewed indicates that episodic memory, as mediated by the HPC, contributes more to language and semantics than classical views on dissociable multiple memory systems would lead us to believe. As with perception and WM, we do not wish to end by obliterating distinctions that we believe are still useful; rather, based on our component process model, we propose that the systems are much more interactive than we once thought, enabling episodic memory and the HPC to influence functions outside their traditional domain. This interactive approach is increasingly evident in neuroimaging research, with its current emphasis on networks and on structural and functional connectivity among nodes in those networks.

PROCESS-SPECIFIC ALLIANCES SUPPORTING EPISODIC MEMORY


The individual brain regions discussed in the previous sections cannot support episodic memory unless they interact with each other and with other regions. In functional neuroimaging studies, these interactions can be indirectly measured as covariation in activity, or functional connectivity. Functional connectivity can be investigated at the level of large-scale networks, such as the default mode network (Andrews-Hanna 2012), or at the level of small networks that are assembled to mediate a specific cognitive operation and rapidly disassembled when the operation is no longer needed. To postulate one of these PSAs (Cabeza & Moscovitch 2013), there should be evidence that (a) all regions in the PSA are associated with the process they are assumed to mediate, (b) each region is associated with a complementary suboperation of this process, and (c) the regions communicate with each other in general and during the process of interest. There are many examples of PSAs that contribute to episodic memory and fulfill these criteria; here, we mention only two.

The first example is the PSA between the pHPC and VPC during recollective retrieval. Consistent with the first criterion, meta-analyses of event-related fMRI studies have strongly linked these regions to retrieval success and recollection (Cabeza et al. 2012). During retrieval, the pHPC and VPC show a recollection-related activity pattern, whereas a very different pattern emerges in the aHPC (e.g., Daselaar et al. 2006) [**Supplemental Figure 10** (follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>)]. In keeping with the second criterion, the pHPC has been linked to the recovery of episodic memory details



and the VPC to the complementary process of operating on the recovered information (Cabeza et al. 2012). Finally, fulfilling the third criterion, the pHPC and VPC have direct white-matter connections and interact very closely during rest and during episodic recollection (Cabeza et al. 2012).

Another example is the PSA between the HPC and domain-specific posterior cortices during encoding and retrieval. Consistent with the first criterion, activity in domain-specific cortices has been associated with successful encoding of relevant stimuli and with the reactivation of this information during retrieval (Danker & Anderson 2010). Second, HPC lesions yield global memory deficits, whereas cortical damage yields domain-specific memory deficits. Finally, the HPC and domain-specific cortices are anatomically linked, and there is evidence that they are functionally connected during rest (Schlichting & Preston 2014) and during successful encoding and retrieval processes (e.g., Ritchey et al. 2013) [**Supplemental Figure 11** (follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>)].

 Supplemental Material

Given that PSAs are rapidly assembled and disassembled, they require a mechanism that can quickly control communication between distant brain regions, and the most likely candidate is neuronal oscillations. There is abundant evidence that oscillations, particularly those in gamma (40–100 Hz) and theta (4–8 Hz) frequencies, control PSAs during episodic encoding and retrieval (Nyhus & Curran 2010). During encoding, gamma phase synchronization helps bind perceptual features into objects in posterior cortices (Engel et al. 1991), and gamma-theta coupling helps integrate objects into events in the HPC and posterior cortices (Jensen & Lisman 2005). In animal studies, HPC theta has been linked to successful spatial learning (Ekstrom et al. 2001) and to long-term potentiation (Hyman et al. 2003). In human studies, successful encoding has been associated with both gamma (Osipova et al. 2006) and theta (Long et al. 2014) frequencies in the HPC and posterior cortices. The coupling is assumed to be controlled by the PFC, and as WM load increases, theta power increases in frontal-midline electroencephalography (EEG) electrodes (frontal-midline theta) (Jensen & Tesche 2002). Moreover, an intracranial EEG study found phase-amplitude coupling between theta and beta-gamma when faces were maintained in WM (Axmacher et al. 2010).

During retrieval, access to a fraction of the HPC representation of the original event is assumed to cause reinstatement of the associated theta cycle, which triggers the reinstatement of the nested gamma cycles and their associated cortical representations (Jensen & Lisman 2005). In keeping with this hypothesis, human studies have found greater gamma and theta (Osipova et al. 2006) power in the HPC and posterior cortices for correct old responses than for new ones. There is evidence of greater gamma power for remember than for know responses in several scalp locations (Burgess & Ali 2002). One of these locations is the parietal cortex, consistent with the aforementioned PSA between the pHPC and the VPC.

In sum, the HPC can only support episodic memory if it interacts very closely with other regions. Each episodic process is mediated by a transient collaboration between regions mediating complementary operations, or PSA, consistent with our component process model. PSAs require a mechanism that can rapidly turn on and off interactions among distant regions, such as neural oscillations in gamma and theta frequencies (Johnson & Knight 2015), and our understanding of these PSAs may help distinguish between recurrent retrieval and re-encoding processes (Ben-Yakov et al. 2014).

CONCLUSION

Since its inception, the scientific study of memory has been influenced by the research program of its pioneers. Ebbinghaus [1964 (1885)] wished to study memory's essence, isolated from the

influence of any other mental function. Bartlett (1932), on the other hand, saw memory as inextricably tied to other mental functions, and often operating in their service. To accomplish his goals, Ebbinghaus used nonsense syllables as memoranda, whereas Bartlett used complex verbal and pictorial stimuli. Given Ebbinghaus's memoranda, memory could only be seen as strengthened or lost (forgotten). Memory for Bartlett's material, on the other hand, could also be transformed with time and experience to reflect the cultural and personal schemas of the person. Memory is the only topic covered in Ebbinghaus's classical book, whereas Bartlett's reads like a book in social psychology. Indeed, Bartlett eschewed the word memory since it implied something static, preferring instead to title his book *Remembering* to reflect an active, adaptive, and changing process akin to other actions we perform. In this regard, his view was closer to that of James [1950 (1890)], who was concerned with the phenomenology of memory and had a functionalist approach to psychology. Although this review has discussed elements of all three perspectives, it has focused especially on Bartlett's and James's. At this time, it would be surprising if it were otherwise, given how interactive brain regions are with one another and how new technological advances drive this point home. We should take care, however, not to lose sight of the trees while our attention is directed toward the interactive forest.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The writing of this article and some of the research reported herein were supported by grants to M.M. and G.W. from the Canadian Institutes for Health Research (grant MGP 6694) and from the Natural Sciences and Engineering Research Council of Canada; to L.N. from NIH, NSF, and the LuMind Foundation; and to R.C. from NIH-NIA (AG19731). The authors gratefully acknowledge the support of the following people: Nick Hoang in preparing the manuscript; Yadin Dudai, Jessica Robin, and Talya Sadeh for their helpful comments; and Dan Schacter for his suggestions, encouragement, and patience.

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