How Hippocampal Memory Shapes, and Is Shaped by, Attention

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Abstract Attention has historically been studied in the context of sensory systems, with the aim of understanding how information in the environment affects the deployment of attention and how attention in turn affects the perception of this information. More recently, there has been burgeoning interest in how long-term memory can serve as a cue for attention, and ways in which attention influences long-term memory encoding and retrieval. In this chapter, we highlight this emerging body of human behavioral, neuroimaging, and neuropsychological work that elucidates these bidirectional interactions between attention and memory. Special emphasis will be given to recent findings on how the quintessential "memory system" in the brain—the hippocampus—influences and is influenced by attention.

Introduction

At one time or another, we have all puzzled over why some things are easily remembered and others are frustratingly forgotten. This question is not just one of casual introspection, but also one that has intrigued and stumped cognitive neuroscientists for decades. Studies of memory behavior have long established that the way we direct our attention strongly determines what we encode into memory. Yet, how attention influences mnemonic processes in the brain has only been investigated more recently. In fact, despite its clear importance for the encoding of new memories, research on how attention modulates the hippocampus is only just beginning. These efforts have coincided with growing interest in how

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memory in turn influences attention. This work has led to the exciting discovery that hippocampal memories can have powerful effects on how we move our eyes and orient our attention. That hippocampal representations can influence attentional processing in this way provides a compelling demonstration of the reach of the hippocampus beyond explicit memory. In this chapter, we provide a review of these bidirectional interactions between hippocampal memory and attention. In the first section, we discuss how attention affects memory encoding and retrieval at the behavioral and neural levels, and how attention modulates the hippocampus in the absence of demands on long-term memory. Then, we turn to how hippocampal memories guide attentional allocation and eye movements during visual exploration, highlighting the influence of both explicit and implicit long- and short-term memories. We end by discussing future directions for research on the interplay between attention and memory, including studies of network connectivity, neuropsychology, neurofeedback, and neuromodulation.

How Does Attention Influence Hippocampal Memory?

Behavioral Studies

Memory comes in different forms. Imagine someone says “hi!” to you in a local coffee shop, and you subsequently try to remember if you’ve seen this person before. You can make that decision based on different types of information. In some cases, you may be able to *recollect* specific, qualitative details about who this person is or when you last saw them—e.g., that this person is your new neighbor, who you met last week. Alternatively, you may be unable to bring to mind details about who the person is, but they nevertheless seem *familiar*—you have seen them somewhere before, but you do not remember where or when. These different types of memory differentially tax hippocampal processing: recollection, but not familiarity, is critically dependent on the hippocampus (for review, see Yonelinas et al. 2010).

A rich body of literature on behavioral expressions of memory has shown that dividing attention impairs performance primarily on those types of memory that are dependent on the hippocampus, such as recollection (Chun and Turk-Browne 2007). For example, dividing attention during encoding—by having participants make judgments on the pitch of auditory tones while encoding a list of visually presented words—impairs subsequent memory judgments made on the basis of episodic recollection, but not memory based on a general feeling of familiarity (Gardiner and Parkin 1990). Subsequent research confirmed that divided attention at encoding produces large impairments in hippocampally-mediated forms of memory (e.g., Craikm et al. 1996; Fernandes and Moscovitch 2000; for reviews, see Craik 2001; Yonelinas 2002).

Although divided attention at encoding impairs memory, early studies suggested that divided attention at retrieval is less detrimental (Craik et al. 1996; Craik 2001). Later studies, however, found that divided attention does interfere with memory retrieval when the concurrent task depends on the same representations (e.g., verbal distracting task and verbal memory retrieval; Fernandes and Moscovitch 2000). Moreover, a review of the literature suggested that divided attention at retrieval produces impairments in recollection-based, but not familiarity-based, memory (Yonelinas 2002). Indeed, the mere presence of task-irrelevant, distracting information can impair episodic memory (Wais et al. 2010), even when the distracting information is in a different sensory modality (Wais and Gazzaley 2011).

In contrast to the extensive literature on divided attention and memory, relatively little work has been done on how *selective* attention influences memory. In divided attention studies, attention is split between the memory task and an unrelated secondary task, both of which must be performed concurrently. In selective attention studies, attention must be used to select one stimulus for further processing amongst other stimuli that need to be ignored. An early example is the dichotic listening paradigm (Cherry 1953), in which participants verbally shadowed one of two auditory streams, each presented to one ear. Participants had essentially no memory for information in the unattended auditory channel (Moray 1959), showing that selective attention strongly gates what is encoded into memory. Selective attention can also apply to different representations of the same stimulus—for example, the meaning versus sound of words. Studies that encourage participants to direct attention selectively to one characteristic of a stimulus while ignoring others have found effects on memory: When the task at retrieval orients participants to the sound of words, memory is better when sound was attended during encoding; in contrast, attention to the meaning of words during encoding produces better memory in a standard recognition task, which is assumed to rely on word meaning (Morris et al. 1977).

Selective attention is especially important when stimuli are in strong competition with one another. For example, with composite stimuli that consist of superimposed faces and scenes, participants show above-chance memory only when the tested aspect of the composite stimulus (e.g., a scene) was selectively attended during encoding (Yi and Chun 2005). Finally, memory is superior when to-be-encoded objects appear in spatial locations at which attention has been selectively directed, compared to unexpected or neutral locations (Turk-Browne et al. 2013; Uncapher et al. 2011).

Attentional Modulation of the Hippocampus

Despite the abundant evidence that attention influences behavioral expressions of episodic memory (also see Hardt and Nadel 2009), how this modulation occurs in the brain is only just starting to be understood (Posner and Rothbart 2014). There are at least two potential routes by which attention might modulate memory. The first, and perhaps prevailing, view is that attention modulates hippocampal memory as a downstream consequence of its effects on sensory representations. According to biased competition models (Desimone 1996), information that is selected by attention is more robustly represented in sensory systems, and thus fares better in competition with unattended information for downstream processing. This biased competition is often manifest as higher levels of activity in visual regions that code for attended features or locations, or sharper, more precise representations of attended information (Gilbert and Li 2013; Kastner and Ungerleider 2000; Maunsell and Treue 2006; Sprague et al. 2015). Thus, according to this framework, strengthened sensory representations are more likely to be transmitted downstream to the hippocampus for further processing, either as items to be encoded or as retrieval cues for existing memories.

A different potential route is that attention directly modulates the hippocampus itself. However, in contrast to the robust effects of attention on sensory cortex, there has been little evidence of attentional modulation in the hippocampus in tasks with no overt demands on long-term memory. Indeed, studies that have manipulated attention to locations (Yamaguchi et al. 2004) and stimulus categories (Dudukovic et al. 2010) while participants underwent functional neuroimaging have failed to observe attentional modulation of the hippocampus. Instead of concluding that there are no direct effects of attention on the hippocampus outside of memory tasks, we recently suggested that these effects exist but were missed in prior studies because of how attention was manipulated and measured (Aly and Turk-Browne 2016a).

The traditional way of studying neural effects of attention is to manipulate attention to relatively simple features or locations, and to measure the effects on the representation of those features or locations in the brain (Kastner and Ungerleider 2000; Maunsell and Treue 2006). For example, participants might be cued to pay attention to the left or right side of fixation, while neuroimaging is used to measure brain activity in areas of early visual cortex that respond selectively to the left or right side of space. Such an approach is sufficient for studying sensory cortex but may be inadequate for studying the hippocampus, whose representations are fundamentally relational and contextual, consisting of (often multimodal) associations between items and the spatial and temporal contexts in which they occur (Brown and Aggleton 2001; Bussey and Saksida 2005; Cohen and Eichenbaum 1993; Davachi 2006; Graham et al. 2010; Ranganath 2010; Yonelinas 2013). Thus, in order to study attentional modulation of the hippocampus, one might have to study the types of relational information that it represents, rather than simple features or locations.

The signature of attention may also be different in cortex vs. hippocampus. In sensory areas, the primary measure of attentional modulation has been the overall level of activity, whether measured with single-cell recordings in animals or functional neuroimaging in humans (Gilbert and Li 2013; Kastner and Ungerleider 2000; Maunsell and Treue 2006). In the hippocampus, however, attentional effects may more strongly manifest as changes in *representational stability*. That is, attention may modulate the reliability of activity patterns in the hippocampus, as opposed to the overall strength of a scalar signal (cf. Dudukovic et al. 2010; Yamaguchi et al. 2004). This would produce distinct patterns of activity for different attentional states: Distributed patterns of activity in the hippocampus would be more similar to each other (or more stable) across multiple instances of the same attentional state than across different attentional states. Evidence in support of this hypothesis came first from animal studies (Fenton et al. 2010; Jackson and Redish 2007; Kelemen and Fenton 2010; Kentros et al. 2004; Muzzio et al. 2009b; for reviews, see Muzzio et al. 2009a; Rowland and Kentros 2008) and was subsequently observed by us in functional neuroimaging studies in humans (Aly and Turk-Browne 2016a, b).

In animal models, representational stability is realized as a change in the reliability of cell firing in the hippocampus as a function of the task relevance of particular aspects of the environment. For example, place cells in the hippocampus—which fire when an animal is in a particular location (Ekstrom et al. 2003; O'Keefe and Dostrovsky 1971)—show increases in the reliability of firing as the task-relevance of spatial cues increases (Kentros et al. 2004; Muzzio et al. 2009b). Conversely, hippocampal cells that respond to odor fire more reliably when olfactory information is task-relevant (Muzzio et al. 2009b). Such representational stability is also observed at the level of networks of cells—for example, different cell assembles consistently activate for different spatial reference frames (Jackson and Redish 2007; Kelemen and Fenton 2010; see also Fenton et al. 2010). Insofar as the environmental cues that animals are orienting to influence, or reflect, their attentional state, this work suggests that attention-like processes may modulate hippocampal representational stability.

Inspired by this work in animal models, we used high-resolution functional MRI to explore the idea of representational stability in human hippocampus—i.e., the notion that attention creates stable and distinct patterns of activity for different attentional states (Fig. 1; Aly and Turk-Browne 2016a). Keeping with the intuition that attentional modulation of the hippocampus might be observed only if attention is oriented to relational information, we designed a novel "art gallery" task in which participants were cued to attend to high-level relations. The stimuli consisted of 3D-rendered rooms, each with a unique configuration of walls and furniture, and a single painting. On each trial, participants were cued to attend either to the paintings (art state) or to the layout of the rooms (room state), as they viewed a stream of rooms with art. On art-state trials, they were to attend to the artistic style of the paintings, in order to identify paintings that could have been painted by the same artist. These paintings were similar in style (e.g., use of color, brushstroke, detail) but not necessarily content. On room-state trials, participants were to attend to the furniture and wall arrangements, in order to identify rooms with the same spatial layout from a different perspective. These rooms had the same configuration of walls and furniture, but different wall colors and furniture exemplars (e.g., a chair would be swapped for a different chair). At the end of the trial, participants had to respond "yes" or "no" as to whether they had found a match. Thus, these tasks emphasized higher-order relations—of abstract artistic style and spatial geometry, respectively—rather than individual features. Importantly, the same stimuli were

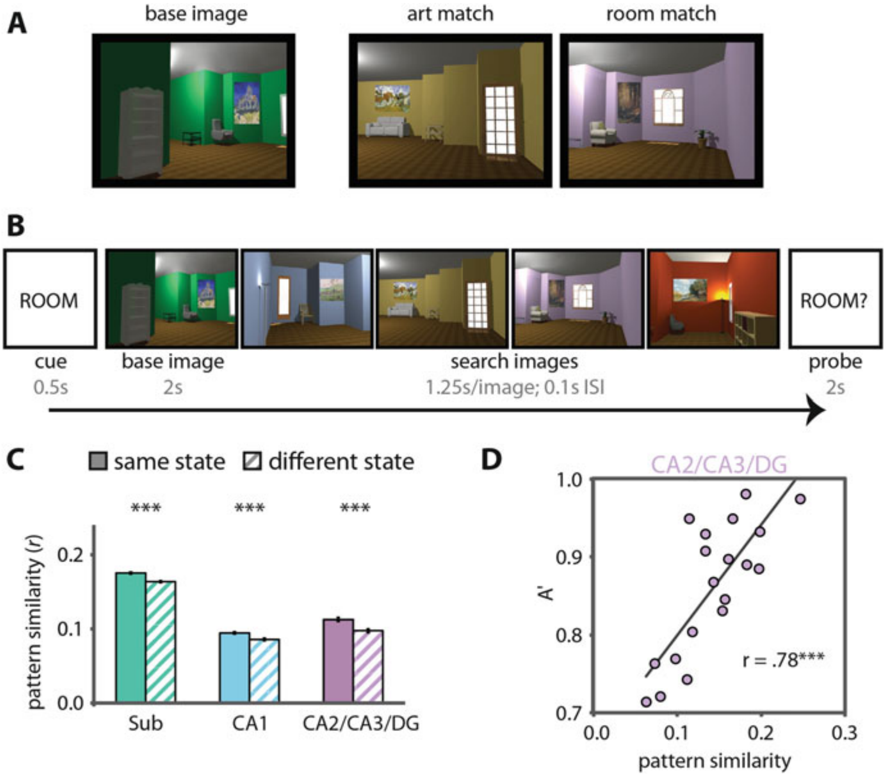

Fig. 1 Attentional modulation of the hippocampus. Attention induces representational stability in the hippocampus, with distinct patterns of activity for different attentional states. (**a**) Stimuli were rooms with a unique layout of walls and furniture and a single painting. For any given "base image", an "art match" was a room containing a painting that was painted by the same artist as the painting in the base image, and a "room match" was a room with the same spatial layout as the base image but viewed from a different perspective. (**b**) On each trial, participants were cued to attend either to the art or to the room. They then viewed a base image followed by a search set of four images. On art trials, participants had to examine the search set for an art match to the base image; on room trials, they looked for a room match to the base image. Finally, they were probed as to whether they found a match, and had to respond yes or no. (**c**) Each hippocampal subfield showed attentional state representations: activity patterns across voxels were more highly correlated for trials of the same (i.e., art/art and room/room) vs. different (i.e., art/room) state. (**d**) Individual differences in the stability of activity patterns in the room attentional state correlated with attentional behavior in the room task. This correlation was selective to the CA2/CA3/DG region of interest, and not observed anywhere else in the brain. ***$p < .001$. Figure adapted from Aly and Turk-Browne (2016a)

used in both tasks, allowing us to isolate the neural effects of top-down attention from those related to bottom-up stimulation.

Consistent with the representational stability hypothesis, we found that attention induced distinct and reliable activity patterns for the two attentional states in each hippocampal subfield: Activity patterns in each hippocampal subfield were more highly correlated for trials of the same attentional state (i.e., art/art and room/room), compared to trials of different states (i.e., art/room). Such representational stability may reflect enhanced processing of the information that is relevant in each state. That is, distinct activity patterns for different attentional states may be a result of prioritizing those hippocampal representations that are necessary for goal-directed behavior in the current attentional state. This prioritization may in turn have consequences for attentional behavior as well as the encoding of goal-relevant information into long-term memory (see section "Attentional Modulation of Hippocampal Encoding").

Indeed, in one hippocampal subfield—comprising subfields CA2/3 and dentate gyrus—individual differences in representational stability for the room state were correlated with attentional behavior on the room task, highlighting the behavioral relevance of attentional states in the hippocampus for online task performance. This brain/behavior correlation was highly selective—it was not found in any other hippocampal subfield, medial temporal lobe cortical region, or anywhere else in the brain. Insofar as attention modulates what we remember, and memory encoding has been linked to CA2/3 and dentate gyrus (e.g., Eldridge et al. 2005; Suthana et al. 2011, 2015; Wolosin et al. 2013; Zeineh et al. 2003), this finding suggests that these subfields may mediate the effect of attention on memory via the creation of state-dependent activity patterns that prioritize goal-relevant information.

We also found that modulation of representational stability was dissociable from modulation of overall activity levels in the hippocampus in a number of ways: For example, overall activity was not correlated with behavior, and voxels with both high activity and low activity contributed to the stability of activity patterns in the hippocampus. Attention also had distinct effects on the hippocampus and medial temporal lobe cortex: Modulation of representational stability in medial temporal lobe cortex was in part due to increases in overall activity. Thus, cortical state-dependent "patterns" differed from those in hippocampus, where a balance of activation and deactivation together produced representational stability. Also, as mentioned above, only attentional modulation of the hippocampus predicted behavior.

These findings provide initial evidence that attention can modulate representational stability in the human hippocampus, and in a way that is relevant for attention behavior. They also suggest that modulation of representational stability might be a means by which attention enhances hippocampally-mediated memory (see section "Attentional Modulation of Hippocampal Encoding").

Attentional Modulation of Hippocampal Encoding

In contrast to the relatively small body of work on attentional modulation in the hippocampus without overt demands on long-term memory, several studies have investigated how attention modulates hippocampal signals related to long-term memory encoding. The dominant signal of interest has been the overall level of activity during encoding, as a function of memory performance on a later test. A *subsequent memory effect* is observed if differential activity at encoding is observed for subsequently remembered vs. forgotten information (Brewer et al. 1998; Wagner et al. 1998). Thus, these studies examine whether univariate subsequent memory effects in the hippocampus are modulated by attention at encoding.

The findings from these studies are mixed: many, but not all, find evidence of attentional modulation of hippocampal encoding. At least some of the null effects might arise from the use of paradigms and methods that are not ideally suited for detecting modulation of hippocampal subsequent memory effects. For example, one early study found no difference in hippocampal activity for full vs. divided attention at encoding (Iidaka et al. 2000). However, this was a PET study, and the slow temporal resolution of this method does not allow isolation of brain activity associated with encoding of individual items that are subsequently remembered vs. forgotten. Indeed, later studies utilizing fMRI—which allows measurement of brain activity related to the processing of individual items—found that divided attention during encoding reduced hippocampal subsequent memory effects (Kensinger et al. 2003; Uncapher and Rugg 2008). Methodological considerations alone do not account for all discrepancies in the literature. For example, an easy vs. hard secondary task at encoding did not modulate hippocampal subsequent memory effects in an event-related fMRI study (Uncapher and Rugg 2005). Another line of work has manipulated the level (or type) of attention by having participants encode items with either a deep (e.g., semantic) or shallow (e.g., phonological) task. Again, data are inconsistent, with some (Otten et al. 2001; Strange and Dolan 2001) but not all (Fletcher et al. 2003; Schott et al. 2013) findings suggesting that hippocampal encoding is sensitive to the attentional depth of processing.

Other studies have more precisely manipulated selective attention at encoding, and have generally observed attentional modulation of hippocampal memory signals. For example, hippocampal activity predicts subsequent memory for words encoded in a relational manner (i.e., when encoding required the formation of inter-item associations), but not those encoded in an item-based manner (Davachi and Wagner 2002; also see Henke et al. 1997, 1999). Moreover, when attention is oriented to one of two contextual pieces of information at encoding—either the location of an object or the color surrounding it—hippocampal activity predicts subsequent memory for the attended, but not the unattended, contextual information (Fig. 2; Uncapher and Rugg 2009).

Selective spatial attention also modulates hippocampal encoding. For example, the hippocampus shows subsequent memory effects for objects that appear in expected, but not unexpected, locations (Uncapher et al. 2011). Moreover, a recent study found that hippocampal subfields CA1 and subiculum showed an interaction between attention at encoding and subsequent memory: Subsequent memory effects were found when participants attended to the distinctiveness of faces at encoding, but not when they attended to their similarities (Carr et al. 2013). In contrast, a combined region of interest for subfields CA2/3 and dentate gyrus showed subsequent memory effects that were comparable for both tasks. These data suggest that

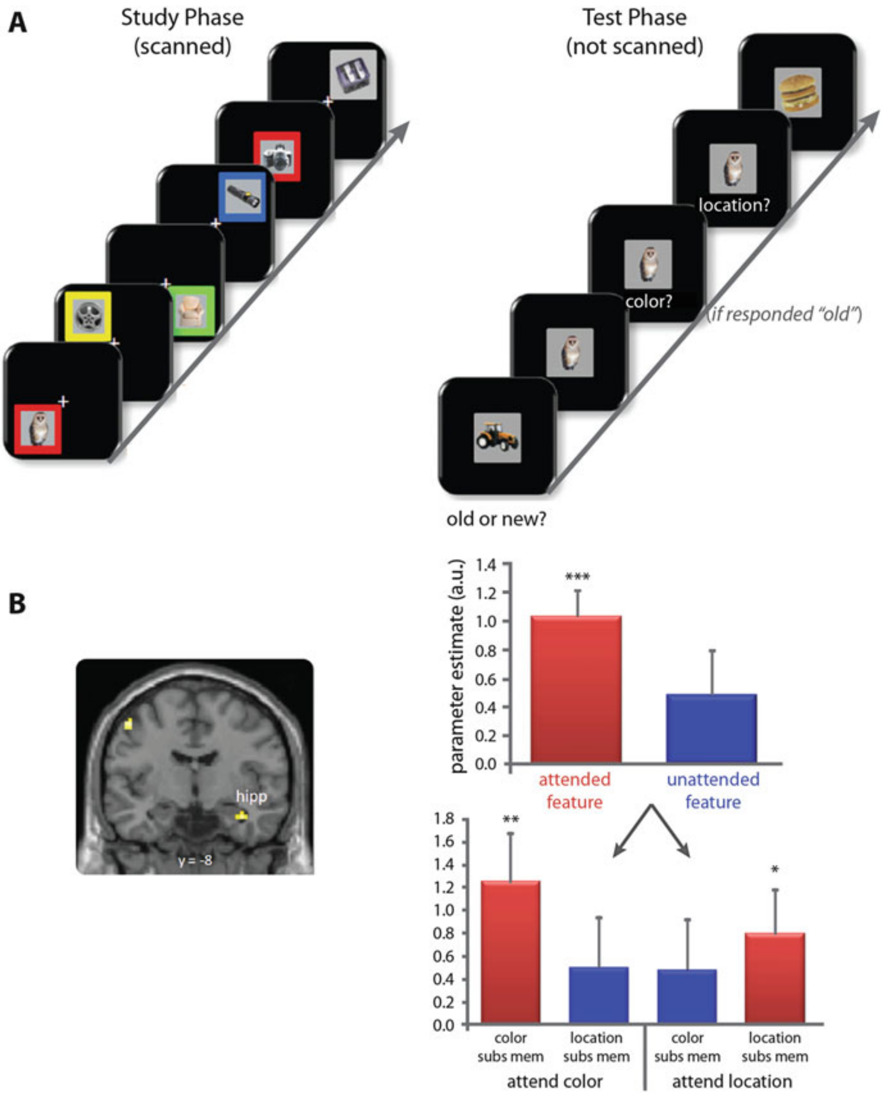

Fig. 2 Attentional modulation of hippocampal encoding. The hippocampus shows a reliable subsequent memory effect only for contextual information that was selectively attended at encoding. (**a**) During encoding, participants attended either to the location of objects on the screen or the color of the border surrounding them. Memory was then tested for the items they encoded as well as the attended and unattended contextual information. (**b**) The overall level of hippocampal activity at encoding was examined based on whether color or location was attended and whether color or location was subsequently remembered. Hippocampal activity at encoding predicted memory (i.e., showed a subsequent memory effect) for attended, but not unattended, contextual information. *$p < .05$, **$p < .005$, ***$p < .0001$. Figure adapted from Uncapher and Rugg (2009)

the mnemonic benefit conferred to distinctive items might arise because of the robust recruitment of the entire hippocampal system.

Thus, studies that manipulate selective attention more consistently find effects on hippocampal encoding than those that divide attention or otherwise manipulate processing resources (e.g., the depth of processing). Why might this be the case? The hippocampus may obligatorily encode information that is consciously apprehended, that is, information in the focus of attention (Moscovitch 2008; Moscovitch et al. 2016). Divided attention manipulations reduce the amount of attention directed toward to-be-remembered information, but may not reduce attention enough to interfere consistently with automatic hippocampal encoding. On the other hand, selective attention manipulations entail processing one aspect of the environment while filtering out others, and this ignored information may not reach the threshold for conscious apprehension necessary for hippocampal encoding.

There is also evidence that voluntary control over attention at encoding confers benefits to memory, and that this effect is dependent on the hippocampus (Voss et al. 2010). Participants memorized objects arranged in a grid by moving a window around the screen that enabled them to view one object at a time, while the rest were obscured. In one condition, participants had volitional control over the movement of the window; in the other condition, they passively viewed the movements made by another participant. Thus, pairs of participants viewed the same objects in the same order, but for one learning phase, they had control over the order in which the objects were viewed; in the other learning phase, they did not. Volitional control over the trajectory of attention during encoding conferred benefits to subsequent memory for the objects as well as their spatial locations. Moreover, hippocampal activity was elevated during volitional vs. passive encoding, and patients with hippocampal damage failed to show the mnemonic benefits of volitional attention. Thus, control over the trajectory of attention is beneficial to memory encoding, and this effect requires the hippocampus.

Together, these findings largely suggest that univariate measures of hippocampal encoding are modulated by attention. However, the reason for inconsistent effects needs to be explored in future studies. One possibility is that in order to observe attentional modulation of hippocampal encoding, attention must be focused on relational information, which is a key component of hippocampal processing (Cohen and Eichenbaum 1993). Indeed, studies that manipulate attention to different types of relations (e.g., Carr et al. 2013; Uncapher and Rugg 2009) or compare relational and item-based processing (Davachi and Wagner 2002; Henke et al. 1997, 1999; cf. Uncapher and Rugg 2006), consistently find effects of attention on hippocampal encoding.

Another possibility is that attentional modulation of hippocampal memory encoding may be more robustly observed when representational stability, rather than the level of activity, is the dependent variable (see Aly and Turk-Browne 2016a and section “Attentional Modulation of the Hippocampus”). Support for this hypothesis comes from a place cell study in rodents, which measured both the rate of firing of place cells as well as the stability of their spatial firing patterns (measured as the correlation between firing rate maps in sequential sessions, where a firing rate map indicates where and how highly a cell fired in a spatial environment). Place fields were more stable when mice engaged in a task that put heavy demands on spatial processing, and this stability correlated with spatial memory (Kentros et al. 2004). In contrast, there were no differences in overall place cell firing rates for tasks that involved high vs. low demands on spatial processing. Moreover, another study found that when rats engaged in "attentive scanning" of a particular environmental location, a place field subsequently formed at that location on the very next pass through it (Monaco et al. 2014), an effect reminiscent of single-shot encoding of a new episodic memory for attended information. Spatial attention therefore modulates the formation and stability of spatial representations in the rodent hippocampus, and predicts the formation and retention of spatial memories.

We recently investigated how hippocampal representational stability during encoding influences episodic memory formation in humans (Aly and Turk-Browne 2016b). Inspired by the rodent studies mentioned above, and our own work showing that attention modulates representational stability in human hippocampus (Aly and Turk-Browne 2016a), we predicted that goal-relevant information would be more likely encoded into long-term memory if the attentional state of the hippocampus during encoding prioritized that type of information. That is, given a particular behavioral goal, attention should serve to focus hippocampal processing on goal-relevant aspects of the environment; to the extent that the pattern of activity in the hippocampus is indicative of being in the goal-relevant attentional state, information pertaining to those goals should be prioritized with respect to online processing as well as transformation into a durable long-term memory.

As in our previous study, we also explored the roles of different hippocampal subfields. We predicted that the attentional state of CA2/3 and dentate gyrus should be most closely linked to successful memory formation, based on studies linking activity and pattern similarity in these subfields to memory encoding (e.g., Eldridge et al. 2005; Suthana et al. 2011, 2015; Wolosin et al. 2013; Zeineh et al. 2003) and based on our finding that representational stability in these subfields predicted attentional behavior (Aly and Turk-Browne 2016a). Thus, the attentional state of these subfields may be particularly important for the attentional modulation of memory.

To test these hypotheses, we designed a three-part study that allowed us to identify attentional state representations in the hippocampus—that is, patterns of activity that are stable across multiple instances of the same attentional state—and then test whether more evidence for the goal-relevant attentional state during encoding predicted subsequent long-term memory (Fig. 3).

While undergoing high-resolution fMRI, participants first completed the "art gallery" task we used in our prior study (Aly and Turk-Browne 2016a) and discussed in a previous section ("Attentional Modulation of the Hippocampus"). On different trials, they attended either to the artistic style of paintings or to the layouts of rooms. We used the neuroimaging data from this part of the experiment

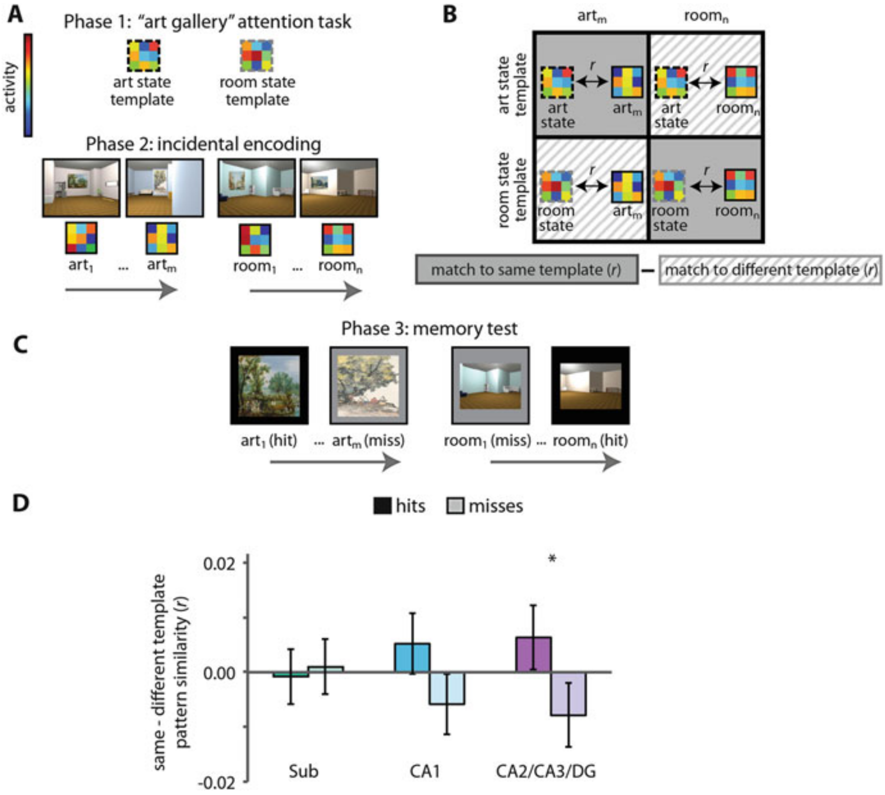

Fig. 3 Attentional modulation of hippocampal encoding via creation of state-dependent activity patterns. The fidelity of state-dependent activity patterns in the hippocampus during encoding predicts memory for goal-relevant information. (**a**) Participants first performed the "art gallery" attention task described in Fig. 1: They viewed images of rooms with art and attended to the artistic style of the paintings or the layouts of the rooms on different trials. From that task, "template" activity patterns for the art and room states were obtained in each hippocampal subfield by averaging activity patterns across all trials of the respective state. Participants then performed an incidental encoding task, viewing trial-unique rooms with paintings and attending to the paintings or the rooms in different blocks. The activity pattern for each encoding trial was extracted from each region of interest. (**b**) These trial-specific encoding patterns were correlated with the goal-relevant attentional state template (e.g., art encoding trial and art state template) and the goal-irrelevant attentional state template (e.g., art encoding trial and room state template). The difference of these correlations measures the extent to which the hippocampus was in the goal-relevant attentional state during encoding, and was the dependent measure of interest. (**c**) These correlation values were binned according to memory in the recognition test that was subsequently completed; that is, each encoding trial was back-sorted as a subsequent hit (remembered) or a miss (forgotten). (**d**) In the CA2/3 and dentate gyrus region of interest, there was greater pattern similarity with the goal-relevant vs. -irrelevant attentional state template during the encoding of items that were subsequently remembered vs. forgotten. This effect was not statistically significant in subiculum or CA1. $*p < .05$. Figure adapted from Aly and Turk-Browne (2016b)

to identify patterns of activity in each hippocampal subfield that corresponded to each of those attentional states; below, we refer to these activity patterns as "templates" for the art state and room state. Participants then completed an incidental encoding task with trial-unique images (rooms with art), attending to artistic style in one block and room layouts in the other. We obtained trial-specific activity patterns in each hippocampal subfield during encoding, and correlated these encoding activity patterns with the attentional state "templates" from the first part of the study. This allowed us to measure the extent to which the activity pattern in the hippocampus on any given encoding trial more closely resembled the goal-relevant vs. -irrelevant attentional state. Finally, participants were tested on their memory for the goal-relevant aspects of the images from the encoding phase: art from the art task and room layouts from the room task.

Consistent with our hypothesis, we found that successful episodic encoding was associated with a better attentional state in CA2/3 and dentate gyrus. That is, during encoding, activity patterns in these subfields more closely resembled the goal-relevant (vs. -irrelevant) attentional state when goal-relevant information was subsequently remembered vs. forgotten. This effect was selective to the hippocampus, and not found in medial temporal lobe cortex or object- and scene-selective regions in ventral temporal cortex (Aly and Turk-Browne 2016b). Together, these data shed light on the mechanisms by which attention transforms what we perceive into what we remember: Attention creates state-dependent patterns of activity in the hippocampus, which serve to prioritize the processing of goal-relevant aspects of the environment and create durable memory traces.

Attentional Modulation of Hippocampal Retrieval

Only a few studies have investigated how attention during retrieval modulates hippocampal memory signals. The initial studies used divided attention paradigms, and—as with the studies of divided attention during encoding—showed mixed results. For example, the PET study mentioned earlier with respect to divided attention during encoding (Iidaka et al. 2000) also found null effects during memory retrieval: Hippocampal activity was not different for full vs. divided attention. In contrast, an fMRI study—also using a blocked design, with no separation of brain activity for particular items as a function of memory success—found a reduction in hippocampal activity for divided vs. full attention during retrieval (Fernandes et al. 2005).

However, studies that have manipulated selective attention by instructing participants about which aspects of a stimulus to attend have consistently found modulation of hippocampal retrieval. For example, one study found evidence that novelty signals (enhanced activity for novel vs. familiar stimuli) in anterior hippocampus are sensitive to attention (Hashimoto et al. 2012). Participants were shown objects in a memory test that were either identical to ones that had been encoded earlier ("Same" items), perceptually different but in the same semantic category

("Similar" items; i.e., if a dog had been studied, a different dog would be included in the memory test), or entirely new ("New" items). Attention at test was oriented to either perceptual or semantic information. For perceptual attention, participants had to respond "old" if an object was perceptually identical to one they had studied, and "new" otherwise. For semantic attention, participants had to respond "old" if an object was perceptually or semantically identical to one they had studied, and "new" otherwise. Thus, a Similar item was called "new" in the perceptual task but "old" in the semantic task. Hippocampal activity for Similar items was comparable to New items in the perceptual attention task, and activity was higher than for Same items. In contrast, for the semantic attention task, Same and Similar items were associated with comparable hippocampal activity, and less activity than for New items. Thus, attention to perceptual vs. semantic information at retrieval modulates what is considered "novel" by the hippocampus.

Another study found converging evidence that novelty signals in the hippocampus are modulated by attention: Posterior hippocampus showed greater activity for correct vs. incorrect memory judgments when participants assessed the relative recency of items, while anterior hippocampus showed greater activity for correct memory judgments when participants assessed their novelty (Dudukovic and Wagner 2007). Moreover, attention to object vs. spatial information during retrieval modulated the response of hippocampal subfield CA1 to the amount of change in a probe item as compared to a similar studied item (Fig. 4; Duncan et al. 2012).

The capacity for the hippocampus to retrieve memories can also be voluntarily suppressed. That is, we can try to control the extent to which a retrieved memory comes to mind by selectively directing attention toward or away from retrieving that memory. Attempts to suppress memory retrieval do in fact worsen memory, and these suppression events are associated with reductions in hippocampal activity (Anderson et al. 2004; Anderson and Levy 2009; Hulbert et al. 2016). Subsequent research has investigated the dynamics that underlie our ability to selectively retrieve information while inhibiting competing information (e.g., Hulbert et al. 2016; Kuhl et al. 2011). In one such study (Wimber et al. 2015), participants learned associations between word cues and two images (e.g., the word "antique" paired with Albert Einstein, and, later, the word "antique" paired with goggles). They then selectively retrieved, in as much detail as possible, the first learned associate given the word cue (i.e., they would have to recall Einstein given "antique"). Presumably, during retrieval, selective attention is directed toward retrieving the target (Einstein), and away from the competitor (goggles). As a result of competitive retrieval, representations of the sought-for memory were strengthened in the hippocampus, while representations of the interfering competitor were weakened.

Another form of competition can come from distracting information. Indeed, the mere presence of task-irrelevant information during retrieval can reduce memory-related signals in the hippocampus (Wais et al. 2010). Bottom-up distraction from irrelevant stimulation can therefore interfere with the ability of the hippocampus to support episodic memory retrieval, perhaps by impairing our ability to selectively attend to task-relevant information.

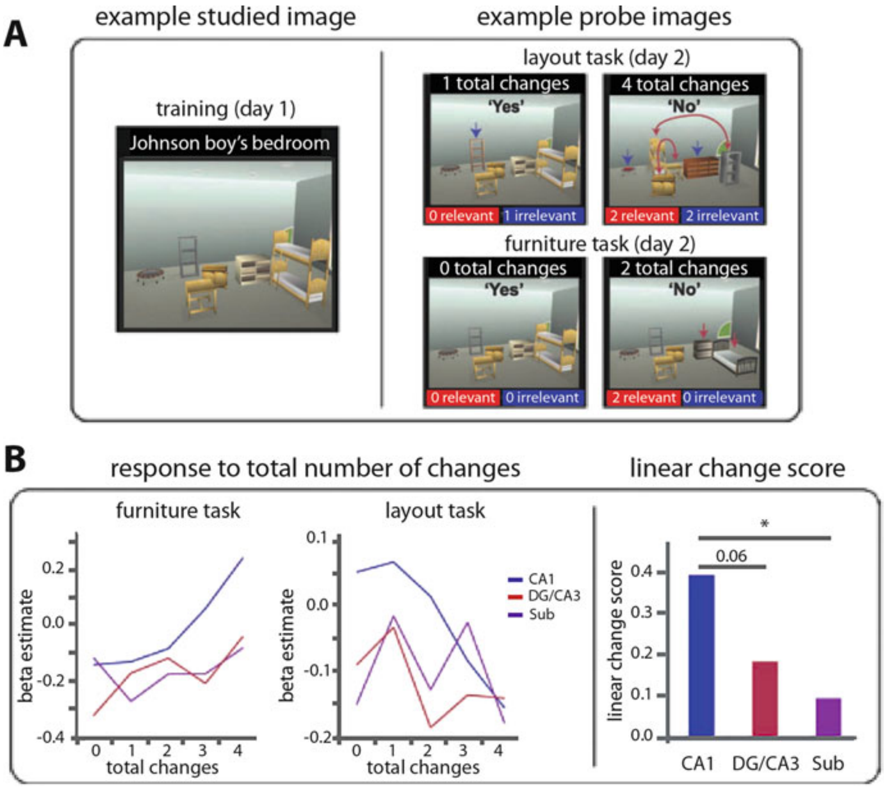

Fig. 4 Attentional modulation of hippocampal retrieval. The response of hippocampal subfield CA1 to associative mismatch at retrieval is modulated by attention. (**a**) Participants learned a set of distinctive rooms with unique furniture layouts. On each test trial, participants were presented with a probe image that corresponded to one they had studied, and performed one of two tasks. For the layout task, they had to indicate if the layout of the room was the same as what they had studied, ignoring any changes to the visual details of the furniture (e.g., if a bookcase was swapped for a different bookcase). On furniture trials, they had to indicate if the furniture was the same as what they had studied, ignoring any changes to the layout. The total number of changes in the probe image consisted of both task-relevant changes (e.g., layout changes on layout trials) and task-irrelevant changes (e.g., furniture changes on layout trials). (**b**) During retrieval, activity in CA1 was monotonically modulated by the number of changes in the probe image. The nature of this relationship differed as a function of attention to furniture vs. layout at retrieval: an increasing trend for the furniture task and a decreasing one for the layout task. *$p < .05$. Figure adapted from Duncan et al. (2012)

Thus, as with encoding, studies that manipulate selective attention more consistently find effects on hippocampal retrieval than those that divide attention. And, as with encoding, this pattern of results may be related to aspects of hippocampal memory that are relatively automatic. Some stages of recollection are presumed to be obligatory once a cue is consciously apprehended (Moscovitch 2008; Moscovitch et al. 2016). Divided attention studies may not reduce processing resources enough to prevent memory cues from being registered by the brain and triggering rapid hippocampal recollection. Conversely, selective attention, which focuses processing on one aspect of a stimulus and filters out others, changes what information is consciously apprehended, perhaps leaving some information below threshold for rapid hippocampal retrieval.

Another possible reason for why some studies fail to find effects of attention on hippocampal retrieval is that, in at least some situations, attention only has transient effects on hippocampal activity (Vilberg and Rugg 2012; also see Vilberg and Rugg 2014). In one study, participants studied word-picture associations and later had to remember the picture given the word as a cue. They were told to maintain the picture in mind over a delay, until a prompt appeared indicating which of three judgments had to be made about the remembered picture. Thus, the delay period served as time during which attention had to be focused on the contents retrieved from memory. Hippocampal activity related to successful recollection was transient—it did not persist during the delay, but was momentarily elevated after the appearance of the word cue. In contrast, elevated activity related to recollection was sustained over the delay in the intraparietal sulcus and angular gyrus, among other regions. Thus, the effects of maintaining attention to retrieve information from memory may only transiently engage the hippocampus, perhaps reflecting an initial, rapid recollection process (Moscovitch 2008; Moscovitch et al. 2016), while parietal cortical activity may be sustained because it indexes the amount of retrieved information (Vilberg and Rugg 2007).

How Do Hippocampal Memories Guide Attention?

Episodic Memory and Attention

We now turn to the other side of the story relating the hippocampus and attention—how hippocampal memories affect attentional orienting (Hutchinson and Turk-Browne 2012). We begin with studies showing that episodic memories can serve as guides for the allocation of attention during visual search and visual change detection (Hollingworth 2006).

In classic visual search paradigms, participants look for a particular, pre-defined target and respond as quickly as they can when they find it. One way of studying the influence of memory on target detection is by comparing search times for targets in new contexts to search times for targets in familiar contexts (Chun and Jiang 1998). For example, participants are faster at detecting targets in a fixed location within a real-world scene that is repeated vs. novel, with responses getting progressively faster across scene repetitions (Brockmole and Henderson 2006). This facilitation of visual search is accompanied by episodic memory for the repeated scenes (i.e., above chance recognition accuracy), as well as accurate recall of the specific target position within the scenes. Moreover, "previewing" a scene before performing a visual search task facilitates the detection of a target object (compared to a no-preview baseline), whether or not the previewed scene actually contains the target object (Hollingworth 2009). Thus, visual search is facilitated both by memory for specific goal-relevant object-location associations as well as memory for the general context.

This facilitation of visual search by long-term memory has been linked to the hippocampus (Fig. 5; Stokes et al. 2012; Summerfield et al. 2006; cf. Rosen et al. 2015). In these studies, participants have to search for a particular target—e.g., a key—in a visual scene. Information about where the key might be is provided either by memory or by perception on different trials. On memory-cued trials, participants had, on the previous day, learned the location of the key for that particular scene. Thus, they could rely on long-term memory in order to guide attention to the previously learned location of the key. Memory could also be uninformative, however—some scenes, although studied on the previous day, had never contained a key. On perception-cued trials, a box was presented on the screen around the location of the key, so that this visual cue could be used to direct attention. This visual cue could also be uninformative, however—on some trials, it could be presented at the center of the screen, and not around the key.

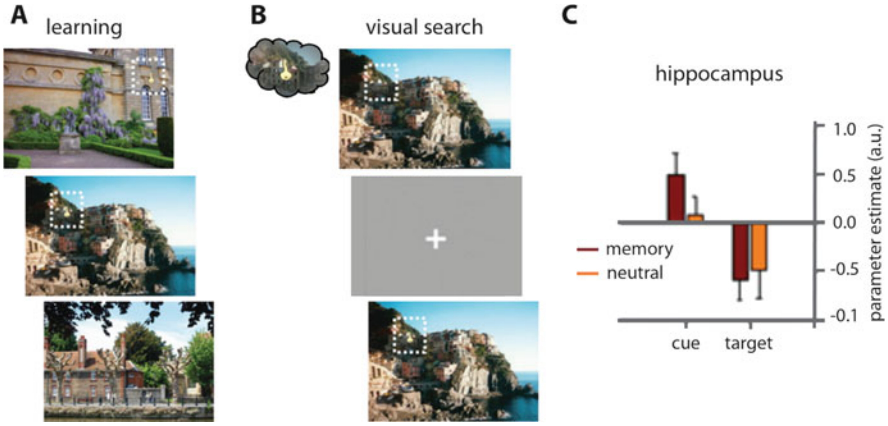

Fig. 5 Attentional guidance by episodic memory. The hippocampus is recruited for visual search cued by explicit long-term memory. (**a**) In the first phase of the study, participants explored a set of scenes, looking for a key in each. During this learning phase, therefore, associations were formed between particular scenes and the location of the key. Other scenes did not contain a key. (**b**) The next day, participants performed a visual search task with scenes that had been encoded the previous day, detecting the brief appearance of a key in those scenes (the key was present 50 % of the time). On memory-cued trials, the scene had contained a key when it was encoded on the previous day. On neutral trials, the scene had not contained a key during encoding. The scenes were shown first without a key (i.e., just the scene cue), and then, on target present trials, the key was superimposed. When present on memory-cued trials, the target always appeared in the learned location. Displayed here is an example memory-cued trial with target present. (**c**) The hippocampus was recruited by memory-guided attention, with greater activity for memory-cued vs. neutral trials, specifically during the cue (vs. target) period of the trial. Figure adapted from Stokes et al. (2012)

Both forms of cuing—memory-based and perception-based—conferred benefits to visual search: Participants were faster at responding when those cues were informative vs. uninformative (e.g., Summerfield et al. 2006). Critically, hippocampal activity was higher for trials in which memory provided predictive information about the location of the target vs. trials in which memory was uninformative. Informative perceptual cues, however, were not associated with more hippocampal activity than uninformative ones. In addition, hippocampal activity was more strongly correlated with behavioral benefits from memory cueing than those from perceptual cuing. Because participants were able to recall the target locations, these findings implicate the hippocampus in visual search cued by explicit memory in particular.

Memory for item-context associations is just one way in which memory can guide visual search. Another role for memory is in the maintenance of item representations. That is, even in a novel or changing context, memory for the target(s) of search plays an important role. This is studied in paradigms in which there are many potential targets, and visual search therefore draws upon memory for the set of possible targets. Such tasks are meant to model real-world search situations in which, for example, you go to a soccer game with a group of friends, get separated, and can rapidly scan the crowd for any one or more of them. The visual characteristics of those targets (i.e., your friends) are stored in memory, and the number of friends you are searching for can be thought of as the memory "set size". This can be contrasted to the size of the crowd, which is the perceptual set size. Perceptual set size has a much greater cost for search efficiency than memory set size: As perceptual set size increases, response times increase linearly, whereas as memory set size increases, response times increase logarithmically (Wolfe 2012). Follow-up studies have linked this efficient search process to flexible memory representations: The memories are flexible in that they do not have to perceptually match the sought-for target, and search remains efficient even with few experiences with the item stored in memory (Guild et al. 2014). Concretely, you would still be incredibly efficient at searching a crowd for several people even if you had only been given descriptions of what they looked like, or if you'd seen them before but only once or twice. This efficient search is thought to be mediated by memories retrieved via a rapid form of recollection argued to be an obligatory, unconscious first stage of hippocampal retrieval (Moscovitch 2008; Moscovitch et al. 2016).

The benefits of long-term memory for attentional behavior are not limited to visual search. Memory also facilitates visual change detection—that is, the identification of perceptual changes in scenes. In change detection paradigms, participants view two versions of a scene in alternation (either several times or just once each), and have to identify the difference between the two (Rensink et al. 1997). In one such study, participants first had to detect the addition of a particular object to a scene (Becker and Rasmussen 2008). They were then shown the scenes again, and had to detect the addition of a new object in a new location, the old target object in a new location, or a new object in the old location. Change detection was faster for new objects in old locations, and old objects in new locations, compared to new objects in new locations. Thus, memory for previously goal-relevant objects and locations facilitates visual change detection. Moreover, a recent study found that long-term memory facilitates change detection performance even more when multiple different locations are made goal-relevant by prior experience (Rosen et al. 2014).

Finally, items studied at a particular spatial location (e.g., left vs. right side of a computer screen) subsequently bias attention toward that spatial location, even when they are centrally presented (Ciaramelli et al. 2009). This attentional bias facilitated the detection of dot probes that appeared on the side of the screen associated with the centrally presented item in memory. Furthermore, this facilitation of target detection by memory was correlated with subjective reports of recollection. These results offer further evidence that the contents of episodic memory can automatically, and rapidly, affect the spatial deployment of attention.

Another type of long-term associative memory that can affect the allocation of attention is semantic memory, or general knowledge about the world. For example, knowledge of what objects are typically found in a kitchen can guide how we move our eyes (and attention) as we search for a particular kitchen item (Torralba et al. 2006) and can facilitate the identification of objects that are expected in a kitchen context (Bar 2004). Semantic knowledge is not always helpful, and can even interfere with performance: Visual search is impaired by the presence of distractors that are semantically related to the target (Moores et al. 2003). Moreover, the allocation of attention to semantically related information can be automatic, occurring even when that information is completely irrelevant to the task at hand (Seidl-Rathkopf et al. 2015).

An unexplored possibility is that some effects of semantic memory on attention are at least in part linked to episodic memory. For example, when using memory to guide visual search for a particular kitchen item, you may rely on episodic memory for the last time you were in your kitchen rather than semantic memory of kitchens in general. Whether, and how, semantic and episodic memory interact in guiding attention is unclear. Moreover, whether the effects of semantic memory on attention are ever mediated by the hippocampus—perhaps when access to semantic knowledge is bolstered by episodic memory (Sheldon and Moscovitch 2012)—is currently unknown.

Implicit Learning and Attention

There is evidence that more unconscious knowledge of prior experience can guide attention during visual search, and that such implicit learning might be linked to the hippocampus. When the spatial context in a visual search task consists of a repeated (vs. novel) configuration of simple letters or shapes, rather than a real-world scene as in the studies above, recognition memory is at chance but visual search is still facilitated (Chun and Jiang 1998). That is, targets that appear at fixed locations (or have fixed identities) within repeating configurations of distractor locations

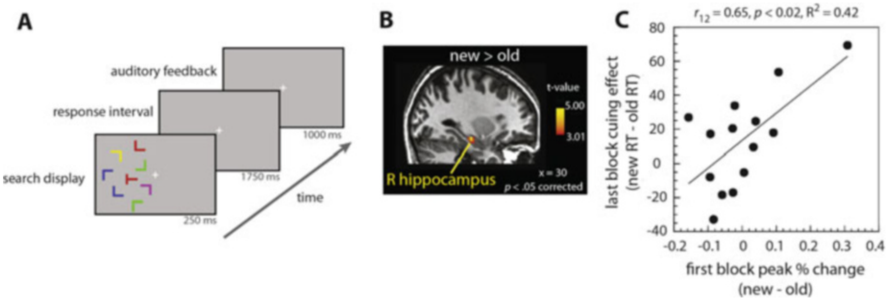

Fig. 6 Attentional guidance by implicit contextual memory. The hippocampus is recruited for visual search cued by implicit long-term memory. (**a**) Participants performed a visual search task in which they had to locate a target (the letter T) amongst distractors (the letter L) and indicate whether the T was oriented 90° clockwise or counter-clockwise. Some search displays were entirely novel ("new" contexts) while others were repeated several times over the experiment ("old" contexts). (**b**) Hippocampal activity was modulated by the type of display, with greater activity for new vs. old contexts. (**c**) Across participants, modulation of hippocampal activity by new vs. old contexts early in learning was correlated with the magnitude of the RT benefit for old vs. new contexts by the end of learning. Figure adapted from Giesbrecht et al. (2013)

(or identities) are more quickly detected than targets in new configurations (Endo and Takeda 2004).

This *contextual cuing* effect seems to depend on the hippocampus. It was impaired in patients with damage to the hippocampus and surrounding medial temporal lobe cortex (Chun and Phelps 1999; Chun 2000; Manns and Squire 2001). It was also impaired following administration of midazolam, which produces temporary amnesia (Park et al. 2004). Moreover, in healthy adults, hippocampal activity measured with fMRI was lower for repeated (vs. novel) configurations, despite chance performance on an explicit recognition task for those configurations, and this activity was inversely related to search response time (Greene et al. 2007). This overall effect was replicated and extended in subsequent studies (Fig. 6; Giesbrecht et al. 2013; Goldfarb et al. 2016; also see Kasper et al. 2015).

However, studies of the role of the hippocampus in contextual cuing are not entirely consistent. One study found a link between hippocampal activity and explicit memory for repeated contexts, rather than search facilitation, but the reverse pattern of results in adjacent perirhinal and entorhinal cortices (Preston and Gabrieli 2008). A potential reason for the discrepancy between studies is explicit recognition memory for the repeated configurations: In the only study that linked the hippocampus to explicit memory rather than implicit configural learning (Preston and Gabrieli 2008), participants showed above-chance recognition memory; this was not the case for the studies that linked the hippocampus to implicit search facilitation (Giesbrecht et al. 2013; Goldfarb et al. 2016; Greene et al. 2007; Kasper et al. 2015). Perhaps when individuals form episodic memories for the repeated configurations, retrieval of these explicit memories overshadows or prevents more implicit hippocampal memories from guiding visual search, especially when the episodic memories are for the configurations per se and not the target locations (cf. Stokes et al. 2012).

Contextual cuing shows that prior experience can facilitate visual search. Experience can confer other processing benefits as well: By learning what types of things should be attended, salient but irrelevant distractors can be better ignored. For example, training of a particular attentional set can carry over to another task, reducing susceptibility to interference from distraction (Leber and Egeth 2006; Leber et al. 2009). This might result from associating the attentional set with the current context (Cosman and Vecera 2013a). If so, then the hippocampus and/or medial temporal lobe cortex—critical for representing contexts and linking items to the contexts in which they occurred (Cohen and Eichenbaum 1993; Davachi 2006; Ranganath 2010)—might mediate this effect. Indeed, amnesic patients with medial temporal lobe damage failed to show it: The patients were able to overcome distraction in the training task, but this beneficial attentional set was not carried over to a subsequent task in the same experimental context (Cosman and Vecera 2013b).

These examples suggest that implicit contextual learning supported by the hippocampus can facilitate attentional behavior when familiar contexts are re-encountered. Another example comes from studies of statistical learning, which refers to our ability to extract structure from the environment and use it to anticipate likely upcoming events (Schapiro and Turk-Browne 2015). Such structure can occur in space (e.g., items that are typically found next to each other in a grocery store) and time (e.g., phonemes that typically follow each other in a particular language). Participants show sensitivity to statistical regularities on a number of implicit measures (e.g., faster reaction times to predicted vs. unpredicted stimuli), but are usually not explicitly aware of the underlying structure (e.g., Turk-Browne et al. 2005, 2009).

Attention is biased toward information streams that contain statistical regularities, suggesting one way that implicit statistical learning can guide the allocation of attention (Yu and Zhao 2015; Zhao et al. 2013). For example, if several task-irrelevant streams of shapes are presented simultaneously in different locations on a screen in between visual search trials, with one stream containing regularities and the others not, search targets are detected more quickly at the location that had contained regularities (Zhao et al. 2013). This attentional bias also exists for features: During visual search, attention is captured by the color of a (task-irrelevant) structured vs. random information stream. These biases can be long-lasting, persisting even if structure is no longer present (Yu and Zhao 2015). Finally, statistical structure can also guide perception and attention during development: Infants look longer at moderately predictable (vs. completely random or overly repetitive) visual and auditory sequences (Kidd et al. 2012, 2014).

Interestingly, the hippocampus seems to be involved in statistical learning. For example, hippocampal activity is enhanced for blocks of stimuli that contain temporal regularities (Turk-Browne et al. 2009) and for individual stimuli that license a prediction about what should appear next based on past exposure to regularities (Turk-Browne et al. 2010). Beyond overall activity, representations in the hippocampus are shaped by statistical learning: Hippocampal activity patterns elicited by objects that are part of the same regularity become more similar to one another (Schapiro et al. 2012). Moreover, damage to the hippocampus and medial temporal lobe cortex impairs statistical learning (Schapiro et al. 2014). However, because this was a single case study and the patient had extensive medial temporal lobe damage, future studies with selective hippocampal lesion patients will be important. Nevertheless, these initial studies linking the hippocampus to statistical learning suggest an additional way in which hippocampal mechanisms can influence attention—by setting up predictions that both facilitate processing of expected stimuli and highlight unexpected stimuli for additional processing (Hindy et al. 2016).

Implicit Memory and the Guidance of Eye Movements

When we move our attention, we also often move our eyes. Thus, eye tracking provides a powerful method to unobtrusively assess where people are directing their attention. Moreover, eye movements provide insight into cognitive operations that are not accessible to subjective awareness and thus to explicit reports (Hannula et al. 2010).

An emerging body of research suggests that hippocampal memories guide eye movements even when those memories are not conscious (for review, see Hannula et al. 2010; Meister and Buffalo 2016). An initial study of this type examined how healthy individuals and amnesic patients moved their eyes when viewing novel scenes, scenes they had viewed previously, and manipulated versions of previously viewed scenes (Ryan et al. 2000). Scene manipulations consisted of the addition, removal, or positional shift of an object. These changes alter the relations among scene components by disrupting the overall configuration of objects in the scene. Eye movements were used to assess memory for items and for relations: Implicit relational memory was measured by the modulation of eye movements to relational changes in scenes, and implicit item memory (where the “item” is the entire scene) was measured by the modulation of eye movements to repeated vs. novel scenes (see also West Channon and Hopfinger 2008). Healthy individuals made fewer fixations to repeated vs. novel scenes, and this eye movement marker of item memory was preserved in amnesic patients. In addition, healthy individuals who were not explicitly aware of relational changes in scenes made more fixations to the altered portions of those scenes. This eye movement marker of relational memory was not present in amnesic patients. Although these findings did not directly implicate the hippocampus in the guidance of eye movements by past experience (although all patients were amnesic, their etiologies were diverse), they inspired further research into how implicit forms of hippocampal memories might guide eye movements, specifically in situations that call for relational processing.

One such study tested amnesic patients with medial temporal lobe damage, most of whom had disproportionate damage to the hippocampus (Hannula et al. 2007).

Rather than measuring eye movements to changes in spatial relations, this study assessed whether hippocampal associative memory in the form of item-context bindings can bias the way people move their eyes. Participants encoded face-scene associations, and were subsequently presented with three equally familiar faces superimposed on a studied scene. Healthy participants spent more time viewing the face that had been studied with the scene, an effect that emerged rapidly—well before any explicit responses were made. This pattern of eye movements, an implicit manifestation of relational memory, critically depended on the hippocampus, as it was not found in the patients. A later study with the same paradigm found that hippocampal activity during the scene cue—before any faces were presented—was higher for trials in which participants subsequently fixated the correct face (Hannula and Ranganath 2009). Amazingly, this effect was observed even when explicit memory failed.

More evidence for implicit effects of hippocampal memories on eye movements came from a study in which participants viewed scenes that were configurally similar, but featurally dissimilar, to scenes previously encoded (Fig. 7; Ryals et al. 2015). These configurally similar scenes were behaviorally indistinguishable from entirely new scenes, in that participants' overt recognition judgments did not differ. Yet, eye movements tended to explore overlapping regions of space for the configurally similar and old scenes, and hippocampal activity correlated with this exploration overlap. This provides additional evidence that implicit memory for spatial configuration, a type of memory often supported by the hippocampus, can influence how attention is allocated, as indexed by eye movement behavior.

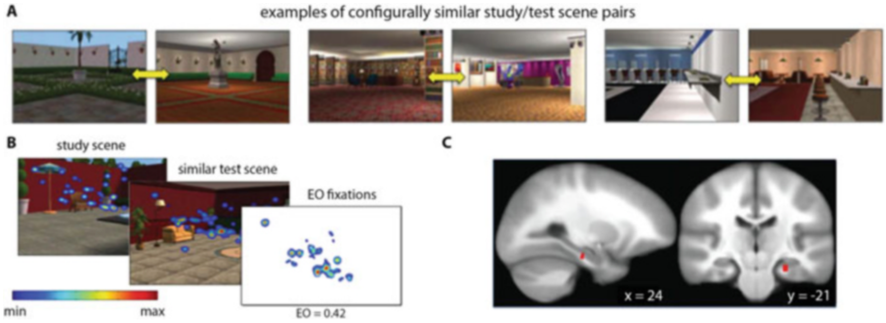

Fig. 7 Guidance of eye movements by implicit configural memory. Hippocampal activity is correlated with eye-movement expressions of implicit configural memory. (**a**) Participants encoded a set of images, and at test were presented with another set of images, half of which were entirely new and the remainder which were configurally similar (but featurally dissimilar) to the previously encoded scenes. Shown here are examples of studied scenes with their configurally-similar matches. (**b**) Example old (studied) scene and its configurally-similar test scene, overlaid with the mean heat map indicating where participants fixated their eyes. Exploration overlap (EO) is a measure of how much fixations overlapped between the studied and similar scenes. (**c**) Hippocampal activity was positively correlated with exploration overlap. Figure adapted from Ryals et al. (2015)

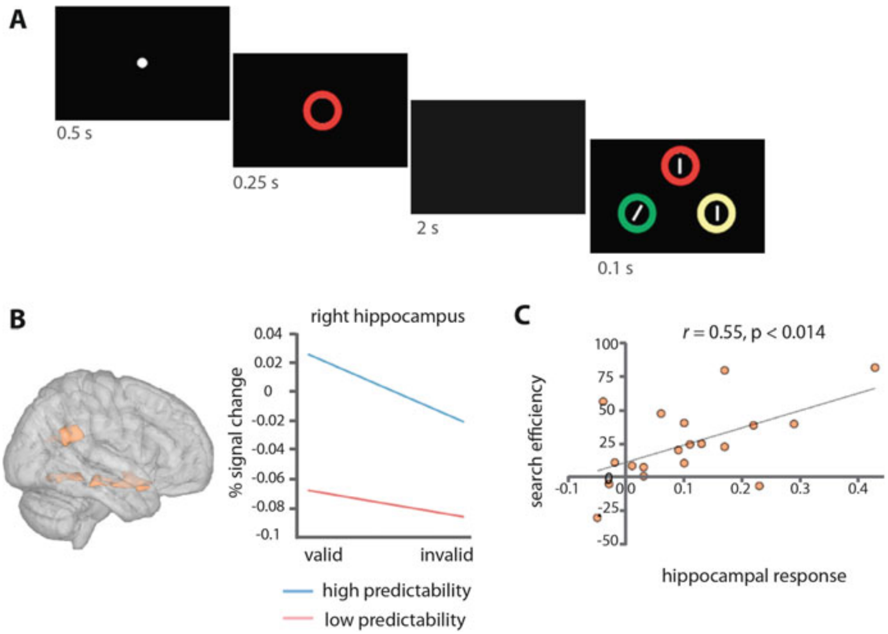

Fig. 8 Attentional guidance by working memory. Hippocampal activity is correlated with the modulation of visual search by the predictability of overlap with working memory contents. (**a**) Participants performed a visual search task in which they had to find the tilted line amongst vertical distractors, and indicate whether it was tilted to the left or the right. Prior to the search display, they viewed a circle—the memory cue—whose color they had to maintain in working memory (on some trials, memory for the color was tested). On valid trials, the circle whose color matched that of the memory cue contained the visual search target. On invalid trials, it contained a distractor. Thus, shown here is an example of an invalid trial. In high predictability blocks, the memory cue was either always valid or always invalid. In low predictability blocks, the cue was valid half the time, and thus could not be reliably used to guide search. (**b**) Hippocampal activity was enhanced for high- vs. low-predictability blocks. (**c**) Across participants, this enhancement was correlated with predictability-related modulation of visual search efficiency. Figure adapted from Soto et al. (2012)

Together, these data raise the possibility that, when a memory cue is presented, the hippocampus retrieves associated information, and these associations in turn guide eye movements (and attention) even when the memory contents do not reach conscious awareness. This view converges with the proposal that hippocampal memory retrieval consists of two stages: The first is rapid and outside of awareness, but can nevertheless affect behavior, while the second is slower, with its output accessible to conscious report (Moscovitch 2008; Moscovitch et al. 2016). These findings suggest that the first stage of hippocampal retrieval has far-reaching effects, directing the movement of our eyes and attention.

An issue for future investigation concerns the role of the hippocampus and eye movements in the facilitation of visual search and change detection by long-term memory (discussed in section “Episodic Memory and Attention”). Long-term memory improves the detection of changes to previously relevant objects and locations in natural scenes, and this is associated with more direct eye movements to those previously relevant objects and locations (Becker and Rasmussen 2008). Likewise, relatively direct eye movements to visual targets are made for familiar scenes in a visual search task (Summerfield et al. 2006). Whether hippocampal activity mediates the relationship between memory, visual search/change detection, and eye movements is an open question.

Working Memory and Attention

Thus far, we have focused on how hippocampal long-term learning and memory influence attention. Recent research has also highlighted a role for the hippocampus in *working* memory—that is, memory over several seconds (for review, see Olsen et al. 2012; Yonelinas 2013). The hippocampus plays a role in working memory for relational or associative (as compared to item) information, and may be particularly important for the maintenance of precise, high-resolution representations (Yonelinas 2013). For example, patients with hippocampal damage are impaired on working memory tasks that require the maintenance of relational information in scenes (i.e., where different scene components are with respect to one another), and this impairment increases with working memory load and retention interval (e.g., Hannula et al. 2006; Jeneson et al. 2011).

Information retained in working memory can attract attention to visually or semantically related items (e.g., Downing 2000; Huang and Pashler 2007; for review, see Soto et al. 2008), raising the possibility that hippocampally mediated working memory can bias attention. Evidence in support of this possibility came from a study that manipulated whether the contents of working memory overlapped with the target of attention, and whether this overlap was predictable or not (Fig. 8; Soto et al. 2012; also see Soto et al. 2007). On each trial, participants were presented with a working memory cue (a colored circle) to maintain over a delay before the brief appearance of a search display of three colored circles, one of which matched the color maintained in working memory. The matching circle contained the search target (a tilted line) or a distractor (a vertical line). Thus, the contents of working memory could either facilitate detection of the target or hinder performance, depending on whether the matching colored circle was around the target or a distractor. In different blocks, the relationship between working memory contents and the search target was manipulated: In predictable blocks, the search target was either always or never in the circle that matched the color in working memory. In unpredictable blocks, the matching circle contained the search target or a distractor with equal probability. Search times were faster when the search target was in a circle whose color matched the contents of working memory. Moreover, search times were faster when the relationship between working memory contents and the search target was predictable. Finally, hippocampal activity was enhanced for predictable vs. unpredictable blocks, and this enhancement correlated with the modulation of behavioral search efficiency by predictability.

One surprising aspect of this study is that the hippocampus is generally not required for working memory when the stimuli consist of simple features (such as colors and shapes) but is more important for working memory tasks that require retention of relational or associative information (Ranganath and Blumenfeld 2005; Yonelinas 2013). How hippocampal damage affects attentional guidance on this task is thus an interesting question for future research. Additionally, comparison of hippocampal involvement for this task vs. tasks that require working memory for more complex relations will be informative.

Conclusions and Future Directions

In this chapter, we discussed several ways in which attention and memory interact in the hippocampus. Attention influences the encoding and retrieval of hippocampally mediated episodic memories. Moreover, attention creates state-dependent patterns of activity in the hippocampus, and these state-dependent patterns predict online attentional behavior as well as long-term memory for goal-relevant aspects of experience. In turn, many forms of hippocampal memories influence attention: Explicit episodic, implicit contextual, and working memories can serve as a cue for attention and guide eye movements. All of these areas are relatively nascent and so will benefit from additional work. We conclude by highlighting four particular methodological approaches that could provide mechanistic insight in future investigations: studies of network connectivity, neuropsychology, neurofeedback, and neuromodulation.

Although our focus has been on the hippocampus, investigations of the interplay between attention and memory would benefit from consideration of the cortical networks with which the hippocampus interacts (Ranganath and Ritchey 2012). The hippocampus receives input—via medial temporal lobe cortex—from occipital, temporal, and parietal cortical regions (Felleman and Van Essen 1991; Lavenex and Amaral 2000), which may be an important means by which cortical perceptual and attentional signals interface with those in the hippocampus, and a means by which hippocampal memories can in turn influence perception and attention. Indeed, hippocampal activity at rest spontaneously fluctuates with that in lateral and medial parietal cortex, lateral and medial temporal cortex, and medial prefrontal cortex (Buckner et al. 2008; Kahn et al. 2008; Libby et al. 2012; Vincent et al. 2008). This connectivity may allow for the exchange of attentional, perceptual, and mnemonic signals in the brain. It will be informative for future studies to investigate how hippocampal-cortical interactions subserve attentional modulation of memory and the mnemonic modulation of attention. For example, coupling between the attentional states of the hippocampus and retrosplenial cortex has been linked to the modulation of memory by attentional states (Aly and Turk-Browne 2016b).

Another line of investigation for future studies is neuropsychological approaches. Patient studies will continue to yield important insights into the necessity of the hippocampus for attentional modulation of memory and for the guidance of attention by memory. Such studies have already made important contributions (e.g., Chun and Phelps 1999; Cosman and Vecera 2013b; Hannula et al. 2007; Ryan et al. 2000; Schapiro et al. 2014), but many of these studies have relied on patients with damage that extends beyond the hippocampus, making inferences about the specific role of the hippocampus difficult. On the other hand, patients with selective hippocampal lesions often only have partial damage, posing additional interpretational challenges if functions are preserved. The key will be to obtain results across a range of patients, and to analyze behavior as a function of the etiology, extent, and precise location of lesions. Moreover, many recent discoveries in the field of attention and memory have relied on functional neuroimaging, and have yet to be tested in any patient population. Insofar as multiple (potentially non-hippocampal) memory systems can influence attention (Hutchinson and Turk-Browne 2012; also see Hutchinson et al. 2016), it remains an important question whether hippocampal damage will eliminate some forms of attentional guidance, or if other systems can support performance.

Another way that causal inferences might be made about interactions between hippocampal memories and attention is via neurofeedback with real-time fMRI (Sulzer et al. 2013). These studies involve giving participants moment-by-moment feedback about overall activity (or the presence of an activity pattern) in a given brain region. This can be done by, for example, showing a participant a dial on the screen and having them try to move it to the left or right based on the activity in a brain region of interest. In this way, researchers can train participants to exert control over, and thus influence the state of, a given brain region. A potentially more powerful approach than using a participant's brain state to move a dial, however, is to have the participant's brain state change the stimulus that is the target of their behavioral goals (deBettencourt et al. 2015). For example, if a participant is making decisions on faces, the pattern of activity in that participant's brain—which is affected by the quality of their attentional state—could be used to degrade or clarify a perceptually noisy face. Such *closed-loop* designs—in which the state of the brain determines the content or timing of stimulus presentation, which in turn influences the state of the brain, then the next stimulus, and so on—provide an enticing method for pseudo-causal investigations with fMRI by manipulating the activity of brain regions hypothesized to be involved in a task. For example, by comparing the effects on attention and memory of real-time neurofeedback from the hippocampus to the effects of neurofeedback from a control region, conclusions can be made about the specific contributions of the hippocampus. That is, by exerting control over activity in the hippocampus, we can more confidently assess whether that activity is necessary for a particular cognitive function. With standard fMRI techniques, one can only say whether a particular type of brain activity is correlated with that function.

Finally, studies of neuromodulatory systems can elucidate the mechanisms by which hippocampal memories and attention influence each other. The hippocampus is modulated by all of the main neurotransmitter systems implicated in attention, including cholinergic, dopaminergic, and noradrenergic systems (Muzzio et al.

2009a; Rowland and Kentros 2008). These systems have strong influences on hippocampal representations of space and on hippocampal memories (Lisman and Grace 2005; Newman et al. 2012; Parent and Baxter 2004). For example, manipulations of acetylcholine and dopamine alter place field stability in the hippocampus (Brazhnik et al. 2003; Kentros et al. 2004), raising the possibility that these neurotransmitters mediate the effects of attention on hippocampal representational stability. Acetylcholine enhances the influence of environmental input on hippocampal processing by amplifying afferent signals and suppressing excitatory recurrent connections in CA3 (Hasselmo 2006; Newman et al. 2012), providing a potential mechanism by which attention can modulate activity patterns in the hippocampus. These and other neuromodulatory influences can be studied with a variety of methods, including magnetic resonance spectroscopy and pharmacological interventions (e.g., administration of neurotransmitter agonists or antagonists) in humans and in animal models. Neuromodulatory studies would be particularly informative because they could shed light on the physiological mechanisms by which attention creates, shapes, and maintains hippocampal representations. For example, if cholinergic modulation is essential for representational stability in the hippocampus, this would suggest that such stability arises as a result of enhancing the influence of the external environment (via afferent signals from entorhinal cortex) and suppressing memory retrieval (via recurrent connections in CA3).

Despite these exciting future opportunities, existing work has already convincingly demonstrated that hippocampal functions cannot be fully described without consideration of attentional processes, and in turn, that our understanding of attention is illuminated and expanded by considering the influence of the hippocampus. This body of literature also convincingly demonstrates the broad reach of the hippocampus beyond explicit memory, showing that its influence pervades even our moment-to-moment attentional behavior.

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