

Escaping the Past: Contributions of the Hippocampus to Future Thinking and Imagination

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Abstract The hippocampus has long been of interest to memory researchers, but recent studies have also implicated the hippocampus in various aspects of future thinking and imagination. Here we provide an overview of relevant studies and ideas that have attempted to characterize the contributions of the hippocampus to future thinking and imagination, focusing mainly on neuroimaging studies conducted in our laboratories that have been concerned with *episodic simulation* or the construction of a detailed mental representation of a possible experience. We briefly describe a multi-component model of hippocampal contributions to episodic simulation, and also consider the hippocampal contributions in the context of a recent taxonomy that distinguishes several forms of future thinking.

Introduction

It is difficult to think of a topic in cognitive neuroscience that has been investigated more extensively than the role of the hippocampus in memory. The range of questions posed about the hippocampus and memory is vast, covering just about all key aspects of memory research: What role does the hippocampus play in the consolidation of memories over time? Is the hippocampus critical for recall of only relatively recent memories, or is it also critical for recalling remote memories? What contribution does the hippocampus make to the initial encoding of memories? Is the hippocampus important for item memories or just for relational/associative

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memories, and is it more important for recollection than familiarity? Is hippocampal involvement restricted to the domain of long-term memory or is it also involved in short-term, working memory? Is the hippocampus critical only for conscious, explicit or declarative memories or does its influence extend to non-conscious, implicit, or non-declarative memories? Does the hippocampus play a special role in spatial memory and knowledge? The list could go on and on.

During the past decade or so, however, the range of questions about the hippocampus has expanded into new domains focusing on future thinking and imagination—topics that had hardly been considered in mainstream hippocampus research in previous decades. This expansion was fueled in large part by a convergence of findings from studies using different approaches and methods that revealed striking similarities between the cognitive and neural processes that support remembering past experiences and imagining possible future experiences. Thus, for example, behavioral studies revealed that remembered past events and imagined future events share phenomenological features, as exemplified by the finding that temporally close events in either the past or future include more episodic, sensory, and contextual details than more temporally distant events (e.g., Addis et al. 2008; D'Argembeau and Van der Linden 2004). Several different populations that show reduced retrieval of episodic details when remembering past experiences exhibit comparable reductions in episodic details when imagining future experiences, including older compared with younger adults (e.g., Addis et al. 2008) as well as patients with Alzheimer's disease (e.g., Addis et al. 2009b), mild cognitive impairment (Gamboz et al. 2010), depression (e.g., Williams et al. 1996), schizophrenia (e.g., D'Argembeau et al. 2008), bipolar disorder (King et al. 2011), Parkinson's disease (de Vito et al. 2012), and post-traumatic stress disorder (e.g., Brown et al. 2014). Linking more directly to the hippocampus, a number of studies have reported that amnesic patients with hippocampal damage also exhibit deficits when imagining future experiences and novel scenes (e.g., Andelman et al. 2010; Hassabis et al. 2007b; Kurzcek et al. 2015; Race et al. 2011; but for evidence of intact future imagining in amnesics, see Squire et al. 2010). Similarly, some evidence from developmental amnesics with hippocampal damage points toward impaired future imagining (Kwan et al. 2010) whereas other studies suggest spared capacities for imagining novel scenes and future scenarios in such patients (Cooper et al. 2011; Hurley et al. 2011). Although the exact reasons for the contrasting findings in hippocampal patients are still being debated (for discussion, see Addis and Schacter 2012; Maguire and Hassabis 2011; Schacter et al. 2012; Squire et al. 2011), numerous neuroimaging studies have shown that when healthy individuals are asked to remember past experiences and imagine future experiences, a common core network of regions is recruited that includes the hippocampus and medial temporal lobes (for review and discussion, see Benoit and Schacter 2015; Buckner and Carroll 2007; Mullally and Maguire 2013; Schacter et al. 2007a; Schacter et al. 2012). These kinds of observations have led to a dramatic increase in cognitive neuroscience research aimed at future thinking and imagination, with much of it directed at attempting to understand what role is played by the hippocampus in these processes, and how it is related to the more traditional role ascribed to the hippocampus in explicit or declarative memory.

We have previously written several reviews that have provided relatively comprehensive coverage of research from many laboratories that has examined hippocampal contributions to imagination and future thinking (Addis and Schacter 2012; Schacter and Addis 2009; Schacter et al. 2012; see also, Buckner 2010; Mullally and Maguire 2013). In the current chapter, we do not attempt to replicate this broad coverage of the entire field. Instead, we will focus mainly on reviewing studies of imagination and future thinking conducted in our own laboratories that have provided evidence relevant to conceptualizing the nature of hippocampal contributions to these processes. In so doing we will attempt to highlight key questions and issues that we have attempted to address, take stock of our findings to-date, and consider critical open questions that we think need to be pursued in future research. Before discussing our experimental observations concerning the role of the hippocampus in future thinking and imagination, however, we will first consider some general conceptual issues that are relevant to our research.

Imagination, Prospecction, and Varieties of Future Thinking

As we have noted, the recent uptick in research concerning the role of the hippocampus in imagination and future thinking is attributable in part to the demonstration of striking similarities between remembering the past and imagining the future in neuroimaging studies, including common activation of the hippocampus. However, as we have discussed elsewhere (Addis et al. 2009a; Schacter et al. 2012), the distinction between “past events” and “future events” in many neuroimaging (and cognitive) studies is confounded with the distinction between “remembering” and “imagining”. Remembered events must, of course, refer to past experiences. However, neural activity or cognitive properties that are associated with “future events” could be associated with “imagined events”, regardless of whether the imagined events refer to the future, the past, or the present (see also, Hassabis and Maguire 2009). In Schacter et al. (2012), we argued that in light of these considerations, it is important to ask whether experiments that examine the relation between remembering the past and imagining the future inform our understanding of the relation between past and future, or whether they inform our understanding of the relation between memory and imagination, regardless of the temporal properties of imagined events. We reviewed relevant evidence and concluded that while there is some evidence of a role for temporal factors—that is, there is evidence that “imagining the future” differs in some respects from “atemporal imagining”—many of the documented similarities between remembering the past and imagining the future reflect commonalities between memory and imagination, independent of temporal factors (Schacter et al. 2012). We will return to this issue later in the chapter in relation to observations of hippocampal activations in neuroimaging studies.

A second general conceptual issue has to do with what we mean when we talk about “imagining the future” or “future thinking”. Thinking about the future—often referred to by the term “prospecction” (Gilbert and Wilson 2007; Seligman et al.

2013)—can take different forms. We (Szpunar et al. 2014a) have recently proposed a taxonomy of prospection that distinguishes among four basic modes of future thinking: *simulation* or the construction of a detailed mental representation of the future; *prediction* or the estimation of the likelihood of and/or one's reaction to a particular future outcome; *intention* or the mental act of setting a goal; and *planning* or the identification and organization of steps toward achieving a goal state. We further proposed that each of these four basic modes of prospection varies in the extent to which they are based on *episodic* or *semantic* information (Tulving 1983, 2002). In the context of our taxonomy, *episodic* refers to simulations, predictions, intentions, or plans concerning specific autobiographical events that might occur in the future (e.g., an upcoming vacation that will take place next month), whereas *semantic* refers to simulations, predictions, intentions, and plans that relate to more general or abstract states of the world that might arise in the future (e.g., thinking about what the world economy will be like 10 years from now). We conceived of this episodic-semantic dimension as continuous (vs. categorical) in order to allow for what we called “hybrid” forms of knowledge that combine episodic and semantic elements, such as personal semantics (Grilli and Verfaellie 2014; Renoult et al. 2012), which involves general but personal bits of knowledge (e.g., “I am a good golfer”) that people can think about prospectively (“e.g., Someday I want to play golf on the PGA tour”).

With respect to the present chapter, it is important to note that most research on the hippocampus and future thinking in our laboratories, as well as in the field more generally, has focused on episodic simulation (Schacter et al. 2008), that is, the construction of a detailed representation of a specific future personal experience. Thus, our discussion will necessarily focus primarily on the role of the hippocampus in episodic simulation. However, towards the end of the chapter we will also briefly discuss research that has provided evidence concerning the involvement of the hippocampus in prediction, intention, and planning. Note also that there is some evidence relevant to our understanding of possible contributions of the hippocampus to semantic simulation. In an early study, Klein et al. (2002) found that an amnesic patient who exhibited impaired episodic simulation of personal future events was nonetheless able to produce semantic simulations regarding problems that might face the world in the future, such as global warming. More recently, Race et al. (2013) showed that amnesic patients with medial temporal lobe damage (including hippocampal damage), and who were characterized by significant deficits in episodic simulation, could generate semantic simulations regarding issues that the world might face in the future. However, Race and colleagues found that these patients were impaired in their ability to elaborate on those issues. Thus, amnesic patients with episodic simulation deficits may also possess fine-grained deficits in semantic simulation, but the exact relation of these deficits to hippocampal function remains unclear, as Klein et al. (2002) did not report any neuroanatomical findings concerning their patient, and only one of the eight patients studied by Race et al. (2013) had damage restricted to the hippocampus (for detailed discussion of issues related to amnesic patients and future thinking, see Addis and Schacter 2012).

The Constructive Episodic Simulation Hypothesis

Our theoretical approach to conceptualizing hippocampal activations during imagination and future thinking has been defined by an idea that we have referred to as the *constructive episodic simulation hypothesis* (Schacter and Addis 2007a, b). This view emphasizes the key role played by episodic memory in supporting simulations of future experiences, although as acknowledged in our recent taxonomy (Szpunar et al. 2014a), it is clear that semantic memory also contributes critically to future thinking (see also Irish et al. 2012; Klein 2013). The constructive episodic simulation hypothesis holds that past and future events typically draw on similar information stored in episodic memory and rely on many of the same underlying constructive processes. Thus episodic memory is thought to support the construction of future events by extracting and recombining stored information into a simulation of a novel event. We have argued that this arrangement is adaptive because it enables past experiences to be used flexibly in simulating alternative future scenarios without engaging in actual behavior. Importantly, there is considerable evidence pointing toward adaptive functions of episodic simulation (for review and discussion, see Schacter 2012).

However, one potential cost of such a flexible system is that it is vulnerable to memory errors that result from miscombining elements of past experiences, such as misattribution and false recognition. Thus, Schacter and Addis (2007a, b) claimed that the constructive, error-prone nature of episodic memory is at least partly attributable to the key role of the episodic system in allowing people to construct simulations of their personal futures by drawing flexibly on elements of past experiences (for related ideas, see Dudai and Carruthers 2005; Suddendorf and Busby 2003; Suddendorf and Corballis 1997). Indeed, recent experimental evidence has shown that when people recombine elements of actual memories into novel simulations of possible experiences, they are sometimes prone to autobiographical memory conjunction errors, where a simulated experience is mistaken for an actual past experience (Devitt et al. 2015). Moreover, experiments by Carpenter and Schacter (2016) have provided evidence linking flexible recombination processes that support an adaptive cognitive function—associative inferences about relations between separate episodes that share a common element (e.g., Zeithamova and Preston 2010)—to source memory errors that result from mixing up elements of these episodes.

The emphasis placed by the constructive episodic simulation hypothesis on flexibly retrieving and recombining information from past episodes into future simulations provides a theoretical link to a conceptualization of hippocampal functions that naturally allows for its contributions to episodic simulation. Specifically, Eichenbaum and Cohen (2001, 2014) have proposed and provided evidence for the idea that the hippocampal region supports relational memory processes that link together disparate bits of information. Schacter and Addis (2007a) argued that these relational binding processes could support the function of recombining elements of information from episodic memory into simulations of events that

might occur in the future, thereby suggesting at least one way in which the hippocampus might contribute to future event simulation. As we will see in subsequent sections, however, there are other ways in which the hippocampus may also contribute to imagining and future thinking.

Hippocampal Activity and Imagining the Future: Initial Observations

Our research on the relationship between remembering the past and imagining the future began with fMRI studies published in 2007, one that provided striking evidence of hippocampal activation during future imagining (Addis et al. 2007) and another that did not (Szpunar et al. 2007). Differences in the experimental designs used in the two studies, however, are the likely source of the different patterns of results regarding the hippocampus.

Our studies had been preceded by a positron emission tomography (PET) study from Okuda et al. (2003) that examined brain activity when people were asked to talk about past or future experiences that were either temporally close (i.e., last or next few days) or distant (i.e., last or next few years). Numerous brain regions showed common activation during these tasks compared with a control task that required semantic retrieval, including the hippocampus and other regions within the medial temporal lobe (MTL). These observations were important in suggesting a hippocampal contribution to future thinking, but the requirement to use a blocked design did not allow analysis of brain activity in relation to specific events. The relatively unconstrained nature of the task also made it difficult to discern whether participants were recalling and imagining specific experiences or providing more generic or semantic information about their pasts and futures. Thus these results could only provide limited evidence for the contribution of the hippocampus to imagining the future.

In an attempt to gain more experimental control over the nature of participants' memories and future imaginings, Addis et al. (2007) used event-related fMRI, which allowed separation of the past and future tasks into two phases: (1) an initial construction phase during which participants were instructed to remember a past event or imagine a future event in response to a cue word (e.g., "dress") and make a button-press when they had an event in mind; and (2) an elaboration phase during which participants mentally generated as much detail as they could about the event. We compared activity during the past and future tasks with two control tasks that required semantic and/or imagery processing. The main result of the experiment was a striking overlap during both construction and elaboration phases (more so during the elaboration phase) in a core network of regions that was similarly active when participants remembered the past and imagined the future, including medial prefrontal, medial temporal, and posterior parietal cortices (for discussion of this core network, see Benoit and Schacter 2015; Schacter et al. 2007a). Most important

for the present purposes, the left hippocampus was robustly engaged during both the construction and elaboration phases in both the past and future tasks. Perhaps even more striking, the right hippocampus was selectively engaged during the construction phase of the future imagining task.

Addis et al. (2007) proposed that the common engagement of the left hippocampus during past and future tasks could reflect the retrieval of episodic details that are required both to remember a past event and imagine a future event. This finding and interpretation is consistent with the traditional characterization of the hippocampus as primarily a “memory region”. However, the selective right hippocampal activation observed for future event construction fits well with the idea from the constructive episodic simulation hypothesis that the hippocampus may support a process of recombining details into a novel event, which is critical when imagining the future but not recruited to the same extent when remembering the past. In the next section, we will consider a series of subsequent studies that have explored alternative explanations and attempted to provide a more stringent direct test of the idea that the hippocampus contributes to recombination processes that are critical to future event simulation.

It is also useful to consider the previously mentioned study on future event simulation by Szpunar et al. (2007) in light of the preceding ideas. Participants were instructed to remember personal past events, imagine personal future events, or imagine events involving a familiar individual (Bill Clinton) in response to event cues (e.g., past birthday, retirement party). Consistent with the results of Okuda et al. (2003) and Addis et al. (2007), there was clear overlap in activity associated with remembering past events and imagining personal events in many core network regions. Importantly, these regions were not recruited to the same extent when participants imagined events involving Bill Clinton, thus providing evidence that the activated core network regions were specifically linked to the construction of events in their *personal* pasts or futures. However, there was no evidence in the experiment by Szpunar et al. (2007) for greater hippocampal activity for personal past or future events than for “Bill Clinton” events. Although we must be cautious about interpreting a negative finding, it is plausible that the “Bill Clinton” control task required the kinds of relational processing and recombining of event details that are associated with hippocampal activation. If so, significant hippocampal activations during the personal event task would not be evident in a comparison with the Bill Clinton control task.

Simulation or Prospection? Further Characterizations of Hippocampal Activity

These early observations established that hippocampal activity can be observed when people imagine future events, but left open many questions concerning how to interpret such activity. In particular, the idea that hippocampal activity during

future imagining reflects, at least in part, recombination processes that are central to episodic simulation and play a relatively more important role in simulation than in remembering, is consistent with the initial results reported by Addis et al. (2007) indicating selective right hippocampal recruitment during construction of imagined future events. Several subsequent studies addressed the issue more directly, and also examined whether such activity is specific to prospection or can be observed when episodic simulations are not focused on the future.

A study by Addis and Schacter (2008) analyzed further hippocampal activity during the elaboration phase of the past and future event tasks that had been reported initially by Addis et al. (2007), focusing in particular on hippocampal responses associated with increasing amounts of rated detail for past and future events. Addis and Schacter (2008) suggested that when participants remember past events, details are primarily *reintegrated* (i.e., details that have been retrieved together previously are further integrated during retrieval), whereas when they imagine future events, additional processes are recruited that involve *recombining* details into a coherent event. Thus, hippocampal responses to increasing detail in past and future events should be distinguishable. A parametric modulation analysis showed that, on the one hand, the left posterior hippocampus was responsive to the amount of detail for *both* past and future events, probably reflecting the retrieval of details from episodic memory that are important for both tasks. On the other hand, a distinct region in the left anterior hippocampus responded more strongly to the amount of detail comprising future events, which we hypothesized reflects the recombination of details into a novel future event. An additional parametric modulation analysis focused on hippocampal responses associated with the temporal distance of events (i.e., recent or remote) in the past and future. Whereas increasing recency of past events was associated with activity in the right parahippocampal gyrus, increasing remoteness of future events was associated with activity in bilateral hippocampus. Addis and Schacter (2008) suggested that the stronger hippocampal response to more distant than closer future events reflects the increasing disparateness of details that participants included in remote future events, which in turn required more intensive relational and recombination processing to integrate these disparate details into a coherent future simulation.

In an attempt to link hippocampal activity and recombination processing even more closely, Addis et al. (2009a) developed a new *experimental recombination paradigm* that more clearly and directly elicits recombination processes than do standard paradigms that only require participants to imagine a future event. While it is typically assumed that participants engage in recombination processing in these standard paradigms, it is also possible that participants simply remember an entire past event and recast it as a possible future event. To address this issue, the experimental recombination paradigm requires participants to create a novel event from three details that they are recombining for the first time in the experiment. The procedure involves multiple stages. First, prior to scanning participants provide a long list of episodic memories comprised of a key *person*, *object*, and *place*. Second, the experimenter randomly recombines details across different memories into novel person-object-place arrangements. Third, during scanning

participants imagine novel future events that include the recombined person-object-place details. A key finding from the Addis et al. (2009a) study was that of robust hippocampal activation when participants recombined event details on imagination trials, effectively ruling out the possibility that prior observations of hippocampal activity during future imagining reflects only recasting of entire actual past events into the future. Moreover, Addis et al. (2009a) also provided evidence that the activity in the right hippocampus was preferentially associated with imagining recombined events versus remembering actual events, in line with earlier observations from Addis et al. (2007).

This study also investigated another key question concerning the characteristics of hippocampal activation during episodic simulation: Is such activity specific to imagining *future* events, or is it more broadly associated with imagination irrespective of temporal considerations? To address the question, Addis et al. (2009a) included conditions in which participants were instructed to use person-object-place cues to imagine events that might occur in the future or might have occurred in the past (but had not). The result was clear-cut: the hippocampus was recruited to a similar extent when participants imagined both future and past events, suggesting that these regions are used for event simulation regardless of the temporal location of the event. These results dovetail nicely with findings from studies by Hassabis and Maguire and their colleagues showing that the hippocampus is strongly engaged when people are asked to imagine atemporal scenes that are not specifically linked to the past or future, suggesting that the hippocampus contributes importantly to a process of *scene construction* that is central to both remembering and imagining (e.g., Hassabis et al. 2007a; for review and discussion, see Hassabis and Maguire 2009; Mullally and Maguire 2013). Note that this scene construction hypothesis is quite similar to the constructive episodic simulation hypothesis, in that both ideas emphasize the contribution of the hippocampus to the construction of mental events. The scene construction idea places greater emphasis on the role of spatial information in constructed events, whereas the constructive episodic simulation hypothesis places greater emphasis on the contribution of the hippocampus to flexible recombination of various kinds of episodic details (e.g., people, objects, actions, places), with less focus on spatial details in particular.

Additional data indicating that the hippocampus serves a role in episodic simulation that is not exclusively prospective comes from studies that used fMRI to probe the neural correlates of *episodic counterfactual thinking* (De Brigard and Giovanello 2012): when people simulate an alternative outcome to a specific event that occurred in their personal pasts. De Brigard et al. (2013a) used a variant of the experimental recombination procedure in which participants initially provided detailed episodic memories of specific past experiences that had a particular outcome (e.g., “Last summer I went horseback riding with my sister in Virginia and I fell off my horse.”). The experimenter then decomposed each memory into three components: a *context* (e.g., Last summer, Virginia), *action* (“Horse riding”), and *outcome* (“Fell off horse”). In the scanner, participants either recalled the memory in response to these three components, or constructed a counterfactual

version of the memory with a different outcome (provided by the experimenter) that could involve changing a negative outcome to a positive one, changing a positive outcome to a negative one, or changing a peripheral detail of the memory that did not affect the outcome. De Brigard et al. (2013a) found that the right hippocampus (as well as many other regions in the core network noted earlier) was recruited during the construction of episodic counterfactual simulations where the outcome of the memory changed (from either positive to negative or vice versa). In a closely related study, Van Hoeck et al. (2013) directly compared brain activity when participants remembered past events, imagined possible future events, or constructed counterfactual simulations in which they mentally changed the outcome of a past event. They found that the left hippocampus was robustly engaged during the past, future, and counterfactual trials compared with a semantic control condition. In addition, Van Hoeck et al. reported that left hippocampus was more strongly engaged during the future than the past condition, thereby extending similar earlier observations from Addis et al. (2007), but did not find evidence for greater engagement of the hippocampus in the counterfactual than in the past condition. They suggested that because counterfactual simulations are more constrained by what actually happened in the past than are future simulations, there might be lesser recombination demand during counterfactual than future simulations.

In a subsequent study, De Brigard et al. (2015) examined counterfactual simulations involving self and others using an experimental paradigm that draws on autobiographical memories of events about which participants felt regret because of the outcome of a choice they made. For example, if a participant reported a memory where they missed an important appointment because they decided to take a bus instead of the subway, in the self condition they would be asked to construct a counterfactual simulation with a different outcome, i.e., “If only I had taken the subway instead of the bus.” There were also several “other” conditions where participants constructed counterfactual simulations about people they knew well, or unfamiliar fictitious individuals. Compared with a control condition in which participants imagined changes to objects, there was evidence for robust recruitment of the right hippocampus and other core network regions for counterfactual simulation involving self and others, thereby extending the earlier results of De Brigard et al. (2013a). In addition, right hippocampus showed increased recruitment for counterfactual simulations about the self, compared with counterfactual simulations about others. Overall, then, the findings from the studies by De Brigard et al. (2013a, 2015), and Van Hoeck et al. (2013) provide further support for the idea that the hippocampus contributes broadly to the construction of episodic simulations of personal events regardless of whether those simulations entail novel future events or altered past events, although there may be important differences between future and counterfactual simulations (see also De Brigard et al. 2013b, for relevant behavioral evidence).

Additional evidence indicating that the hippocampus is not recruited to the same extent for all types of imagined events comes from a study by Addis et al. (2011a) that contrasted imagining (and remembering) specific events, as in the

aforementioned studies, with remembering or imagining general or routine events that occurred frequently in the past or might occur frequently in the future (e.g., reading the newspaper each morning). Given prior evidence that the hippocampus is responsive to the amount of recombined detail in an imagined future event, we hypothesized that the hippocampus would show heightened activity for imagined specific events compared with routine events. If, by contrast, the hippocampus is mainly responsive to the prospective nature of future events, then it should be more engaged during the construction of both specific and general future events compared with past events.

Addis et al. (2011a) replicated the previously discussed finding from Addis et al. (2007) of increased right hippocampal activity for future versus past event construction. Critically, this increased right hippocampal activity was evident only for specific future events; there was no evidence for right hippocampal activity during construction of generic future events. Thus, consistent with results from Addis et al. (2009a) and De Brigard et al. (2013a), these data provide evidence against the idea that right hippocampal activation for specific future events reveals a uniquely prospective function for this region. Instead, it appears to respond to the amount of specific detail contained in an imagined event.

Encoding Processes and Memory for the Future

The studies reviewed in the previous section point toward a close link between hippocampal activity and episodic simulation that includes, but is not restricted to, imagined future events. The evidence is also consistent with the idea suggested by the constructive episodic simulation hypothesis that the hippocampus is linked to flexible recombination of event details. However, another possibility more closely linked with traditional views of hippocampal function is that activation of the hippocampus during episodic simulation reflects successful encoding of a novel simulated event into memory. Several decades ago, the Swedish neuroscientist David Ingvar recognized that in order for a future event simulation to be useful, it is important to encode the simulation into memory so that the information contained in the simulation could be retrieved at a later time when the simulated behavior is actually carried out. Ingvar (1985) termed this process “memory of the future” (for further discussion, see Szpunar et al. 2013). Given extensive evidence that the hippocampus contributes to successful encoding, especially of relational information (for review, see Davachi 2006), it is possible that some or all of the hippocampal activity observed in episodic simulation studies could be attributed to successful encoding.

To address this issue, Martin et al. (2011) used the experimental recombination paradigm described earlier together with a subsequent memory approach, where brain activity at the time of encoding is analyzed according to whether a particular item is subsequently remembered or forgotten on a memory test (e.g., Wagner et al. 1998). One desirable feature of the experimental recombination paradigm is that it

provides a means to assess retention of the details that comprise an episodic simulation: specific details from the simulation can be provided as retrieval cues for other details. In the study by Martin et al. (2011), participants were scanned while they imagined future events involving person-object-place details that the experimenter had recombined from autobiographical memories that participants provided prior to scanning. Ten minutes after scanning, participants were given a cued recall test that included two details from each simulated event, and they were asked to recall the missing third detail (each type of detail served equally often as a cue as a memory target). When participants provided the correct detail, a simulation was scored as “remembered”. When participants did not come up with a detail, or generated an incorrect detail, a simulation was scored as “forgotten”. Of course, failing to generate the missing detail need not mean that the participant completely forgot all aspects of that simulation, but it seems reasonable to assume that participants retained more information from “remembered” than “forgotten” simulations, which is crucial to the logic of the experiment.

Martin et al. (2011) replicated previous findings of hippocampal activation during episodic simulation compared with a control condition. Critically, simulations that were successfully remembered were associated with greater activity at the time of encoding in the right anterior and posterior hippocampus than simulations that were later forgotten. An additional functional connectivity analysis showed that during successful encoding of a simulation, both anterior and posterior hippocampus exhibited connectivity with each other and with other core network regions. By contrast, when encoding was not successful this pattern of connectivity was no longer observed in the posterior hippocampus, whereas the anterior region still exhibited connectivity with the broader core network. Martin et al. (2011, see also Addis and Schacter 2012) suggested that the connectivity of the anterior hippocampus with the broader core network even during unsuccessful encoding might reflect the attempt to construct episodic simulation, even if it is encoded only to a level that is not sufficient to support subsequent recall.

Martin et al. (2011) also reported that successfully remembered episodic simulations were rated by participants during encoding as more detailed than subsequently forgotten ones, and that activity in both anterior and posterior hippocampal clusters was modulated by the level of detail (though the effect was significant only in the anterior hippocampus). Thus the contributions of the hippocampus to encoding success in this context might be related to construction of a detailed simulation of a future event.

Hippocampus, Event Novelty, and Repetition Suppression

Although it has been well established that the hippocampus is involved in future event simulation, not all studies reveal greater neural activity in this region when contrasting future with past events. For instance, Botzung et al. (2008) asked participants to provide detailed descriptions and summaries (e.g., museum-

exposition) of 20 past and 20 future events one day prior to scanning. The summary cues were meant to (re-)evoke past and future events and were subsequently re-presented to participants in the scanner. In contrast to studies discussed earlier (e.g., Addis et al. 2007), there was no indication of greater activity in the hippocampus for the future relative to past events. One possibility for the lack of a future > past pattern in hippocampus was that the novelty of future events as compared to past events had been eliminated by the provision for participants to generate future simulations outside the scanner. As a result, participants in this study may have been simulating memories of actual events and *memories* of simulated events. One implication of this pattern of data is that the hippocampus is involved in constructing *novel* future events.

To test this idea, van Mulukom et al. (2013) had participants simulate novel future events multiple times. Specifically, participants provided details about familiar people, places, and objects from 100 personal memories that were later used to generate 60 person-location-object simulation cues. One week later, these simulation cues were used to evoke 60 novel simulations of future events in the scanner. Critically, each simulation cue was presented three times in order to assess the extent to which hippocampal contributions to simulation were modulated by event repetition. The results of this study showed that, indeed, increases in simulation frequency were associated with decreases in hippocampal response (see Fig. 1), thus showing that hippocampus is especially responsive to initial as compared with repeated simulations of future events. These data suggest that future investigations of the role of the hippocampus in future event simulation should take care to ensure that the simulated events under consideration are sufficiently novel.

In addition to their findings associated with the hippocampus, van Mulukom et al. (2013) found a similar reduction in neural activity across the entire core network of regions generally associated with future event simulation (Benoit and Schacter 2015; Schacter et al. 2007a). This finding makes sense in light of extant work on the concept of repetition suppression, which states that regions or sets of regions responsible for representing particular stimuli demonstrate reduced neural responding with repeated presentations to those stimuli (Grill-Spector et al. 2006;

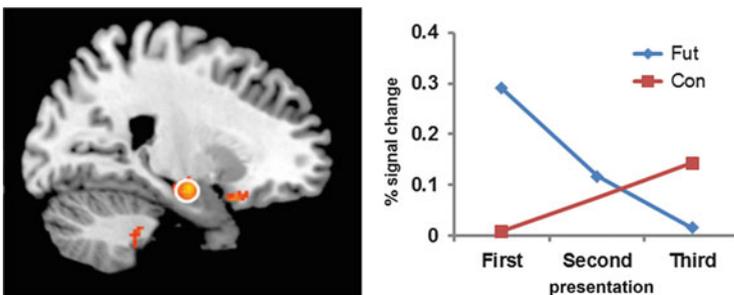


Fig. 1 Reduction in anterior right hippocampal activity across repeated simulations of future simulations (Fut) versus repeated presentations of the control task (Con). Adapted from van Mulukom et al. (2013)

Schacter et al. 2007b). Although prior work on repetition suppression had been mainly conducted using basic stimuli such as pictures of scenes (e.g., Epstein 2008), the results of van Mulukom et al. (2013) clearly demonstrated that a network of regions responsible for representing simulations of complex events abides by a similar principle.

Further evidence that bears on the interpretation of the hippocampal novelty effects reported by van Mulukom et al. (2013) comes from a study by Szpunar et al. (2014b), who assessed whether repetition suppression could be used to isolate the contributions of specific core network regions to future event simulation. Simulations of future events often involve details about people, places, and scenarios that tie those details together. The premise of the study by Szpunar et al. (2014b) was to manipulate the frequency with which specific elements of a complex event were simulated in order to assess which aspects of the core network would show repetition suppression in response to those particular elements. Among other findings, the results of this study neatly demonstrated that regions of the core network commonly associated with representing information about people, such as medial prefrontal cortex (e.g., Raposo et al. 2011), showed repetition suppression when people were repeated but not when locations or scenarios tying people and locations together were repeated. Moreover, regions commonly associated with representing information about places, such as retrosplenial, parahippocampal, and lateral parietal cortices (e.g., Epstein 2008), showed repetition suppression when places were repeated but not when people or scenarios tying people and locations together were repeated. Lastly, regions commonly associated with representing information about social scenarios, such as medial prefrontal, posterior cingulate, temporoparietal and lateral temporal cortices (e.g., Van Overwalle 2009), showed repetition suppression when particular scenarios were repeated but not when people or locations in isolation were repeated. Importantly, as was the case with the results of van Mulukom et al. (2013), Szpunar et al. (2014b) found that the hippocampus was particularly responsive to entirely novel events for which *all* elements (i.e., person, place, and scenario) had not been previously simulated, underscoring once again the link between hippocampal activity and event novelty.

A Multicomponent Account of Hippocampal Contributions to Episodic Simulation and Some Implications

The evidence that we have considered so far indicates that the hippocampus may contribute to episodic simulation in multiple ways. Addis and Schacter (2012) suggested that different regions within the hippocampus might support distinct component processes that play a role in imagining and remembering, including retrieving episodic details, recombining those details into coherent scenarios, and encoding novel scenarios into episodic memory. An important implication of this perspective is that hippocampal activations in neuroimaging studies could potentially reflect the contributions of some or all of these component processes,

depending on the extent to which experimental conditions recruit each component. A further implication is that attempts to isolate the contribution of any one particular component need to control for the potential contributions of the others.

A study by Gaesser et al. (2013) illustrates these points. Gaesser et al. attempted to isolate the contributions of the hippocampus to the process of detail recombination during construction of an episodic simulation by using three procedures: the experimental recombination paradigm and a subsequent memory approach, as in the previously discussed study by Martin et al. (2011), together with a task switching procedure that was used in an attempt to control for novelty processing. As in the Martin et al. (2011) study, participants imagined novel future events based on person, object, and place details taken from autobiographical memories that participants had previously provided. Participants imagined some of these events for the first time in the scanner, and re-imagined other events that they previously imagined the day before. Gaesser et al. (2013) reasoned that events imagined for the first time should require greater recombination processing than re-imagined events because they require the initial integration of disparate details into a coherent simulation, whereas this process has already been carried out once for re-imagined events. However, as discussed in the previous section, simulations that are imagined for the first time are also more novel than re-imagined simulations, thereby making it difficult to determine whether any increased hippocampal activity for newly imagined compared with re-imagined simulations reflects differences in recombination demand or differences in event novelty (Szpunar et al. 2014b; van Mulukom et al. 2013).

Gaesser et al. (2013) attempted to control for such novelty differences by presenting recombined person, object, and place detail sets in a pre-exposure session the day before scanning (participants had provided person-object-place autobiographical memories a week earlier). During this pre-scan session, participants imagined future events for some detail sets and performed a different task—judging the relative pleasantness of the details—for other detail sets. The central idea here is that the novelty of the event details could be held constant across these two conditions by equating pre-exposure to the detail sets. Critically, however, the details were integrated into a coherent episodic future simulation during the imagine pre-exposure condition only; they were not integrated into a coherent episodic simulation in the pleasantness pre-exposure condition. When participants entered the scanner the following day, critical trials involved either switching tasks using the same detail sets as the previous day, or repeating the imagining task. Thus, differences between the imagine condition (i.e., imagine an event for the first time) and re-imagine condition during scanning could be attributed to recombination demand rather than to the novelty of event details in the imagine condition, because event details in this condition had been judged for pleasantness in the pre-scan session.

Ten minutes after the conclusion of scanning, participants received a cued recall test identical to the one used by Martin et al. (2011), in which two event details served as retrieval cues for the third event detail. Gaesser et al. attempted to hold constant encoding success in the neuroimaging analyses by focusing only on

simulations that were successfully remembered. The key analysis thus focused on regions that showed increased activity for the imagine condition compared with the re-imagine condition, examining only successfully remembered items. This analysis revealed an effect in left posterior hippocampus, which Gaesser et al. (2013) attributed to a constructive process of recombining event details into a coherent episodic simulation of a future event. However, Gaesser et al. (2013) also pointed out that the precise localization of this activity differs from observations linking anterior hippocampus, and in some cases right anterior hippocampus, with flexible recombination of event details during episodic simulation (e.g., Addis et al. 2007, 2009a; Addis and Schacter 2008). One possible approach to reconciling the contrasting observations is that the anterior and primarily right-sided hippocampal activity in earlier studies reflects primarily successful encoding of novel episodes, consistent with the aforementioned results of Martin et al. (2011) and other evidence linking the anterior hippocampus with successful associative encoding (e.g., Chua et al. 2007; Jackson and Schacter 2004; Kirwan and Stark 2004; for review and discussion, see Davachi 2006; Poppenk et al. 2013; Schacter and Wagner 1999).

We are hesitant to attempt to draw any firm conclusions concerning the precise localization within the hippocampus (i.e., anterior-posterior, right-left) of component processes that support episodic simulation based on current neuroimaging evidence. We believe that progress on this issue should be facilitated by the use of high-resolution imaging protocols that allow more fine-grained distinctions among hippocampal subfields than are possible with the standard resolution techniques discussed so far (see also, Addis and Schacter 2012). Preliminary evidence along these lines is provided by a study from our laboratory by Stein et al. (2014) using the experimental recombination/subsequent memory paradigm from Martin et al. (2011) together with high-resolution imaging of the hippocampus. Consistent with previous results, Stein et al. found that the CA₁ hippocampal subfield, part of the anterior hippocampus, was associated with successful encoding of simulations into episodic memories. By contrast, activity in the dentate gyrus and CA_{2/3} subfields, which occupy more posterior regions of the hippocampus, was linked with increasingly detailed episodic simulations, which Stein et al. (2014) hypothesized could reflect the operation of retrieval and recombination processes. Thus, although much more evidence is needed before firm conclusions can be drawn regarding intra-hippocampal localization of component processes that support episodic simulation, a preliminary sketch is beginning to emerge. Further research and theorizing on this issue will do well to consider research on episodic simulation in the broader context of studies examining possible function distinctions between anterior and posterior regions of the hippocampus and their connectivity with other brain regions (Poppenk et al. 2013).

Hippocampal Activity During Episodic Simulation in Aging and Depression

In another line of research, we have examined future simulation in populations that exhibit deficits in remembering past events, including older adults and individuals with depression. Consistent with the constructive episodic simulation hypothesis, our general hypothesis for these studies has been that if access to memory is impaired, then a parallel deficit for future simulation should also be evident. Moreover, given hippocampal dysfunction evident in these individuals, the ability to recombine any details accessed from episodic memory should also be compromised. We initially examined these questions across two behavioral studies with healthy older adults, where we used the Autobiographical Interview (AI; Levine et al. 2002) to distinguish between the “internal” or episodic details and “external” or semantic details that comprise autobiographical memories and simulations. In the first study (Addis et al. 2008) we examined the episodic content comprising past and future events generated by younger and older adults in response to single cue words (akin to the design of our first fMRI study described earlier—Addis et al. 2007). Our findings confirmed that older adults showed parallel deficits for past and future events, showing a significant reduction in the number of internal details generated for both past and future events. Surprisingly, however, older adults also exhibited an increase in external content (including semantic details and generic events) for both past and future events, which we suggested might occur to offset the decrease in episodic details or alternatively may reflect a change in communicative goals. Whatever the mechanism underlying the increase in non-episodic content, we had confirmed that the reduction in the episodic content of past events extended to future events.

In a follow-up study, we sought to investigate whether the ability to recombine details into a coherent simulation was also affected in healthy aging (Addis et al. 2010). To this end, we utilized the aforementioned experimental recombination paradigm, using recombined sets of person-object-place details as cues for past and future event trials. We replicated the overall finding of reduced internal and increased external details in descriptions of both past and future events. Importantly, however, the presentation of three simulation details meant we could also determine, for each trial, how many of these critical details were actually integrated into a single simulated event (i.e., one specific event occurring in a specific spatiotemporal context). The key finding here was that older adults integrated significantly fewer details into a single future event than did younger adults, suggesting impaired recombinatory processes likely due to reduced hippocampal function with advancing age.

To directly test the idea that age-related hippocampal dysfunction plays a role in these changes in episodic simulation, we (Addis et al. 2011b) conducted an fMRI study based on our original fMRI task (Addis et al. 2007). Overall, when remembering past and imagining future events older adults engaged many core network regions to a similar extent as young adults. Critically, however, older adults

exhibited reduced activity in medial temporal regions, including the bilateral hippocampus, supporting the notion that reduced hippocampal activation is associated with reduced episodic content of past and future simulations. Indeed, ratings for the amount of detail comprising past and future events was only correlated with hippocampal activity in younger adults. In older adults, detail ratings were associated with increased activity in anterolateral temporal cortex (BA 20), likely reflecting increased non-episodic detail.

Individuals with depression also exhibit parallel changes in past and future events, such that the ability to generate *specific* events (i.e., events that are temporally and spatially specific) is reduced. Instead, depressed individuals typically generate “overgeneral” past and future events (e.g., “I am always late” vs. “I was late to work last Monday due to a traffic jam on the Northern Motorway”). Initially described in suicidally-depressed patients for past events (Williams and Broadbent 1986), this phenomenon has since been observed across the spectrum of depression, in individuals who are subclinically depressed (e.g., Dagleish et al. 2007), dysphoric (e.g., Dickson and Bates 2006), at risk of depression (e.g., Young et al. 2013) or currently in remission (e.g., Brittlebank et al. 1993; Mackinger et al. 2000). Moreover, this overgenerality extends to future events (Dickson and Bates 2006; Williams et al. 1996), consistent with our findings for older adults and the notion that remembering and imagining are closely related.

While much of the literature on overgeneral past and future events has attributed this impairment to the effects of rumination, functional avoidance and executive dysfunction (i.e., the CaRFaX model; Williams et al. 2007), few studies have considered the impact of hippocampal atrophy and dysfunction which is often evident in depression (Campbell and MacQueen 2004; Fairhall et al. 2010). Existing fMRI studies of past events in depression had not controlled for event specificity (Whalley et al. 2012; Young et al. 2012, 2013) and no imaging study had examined the neural correlates of future events in depression. Thus, we conducted a study in which individuals with and without a history of depression retrieved past events and imagined future events (Hach et al. 2014). Importantly, non-specific events were removed from the analysis to ensure specificity was matched, enabling us to compare group differences in the neural correlates of event construction rather than specificity per se. We found that the depression group not only exhibited reduced activity in the right hippocampus, but that right hippocampal connectivity with other core network regions was reduced relative to the control group. However, the depression group did show increased recruitment of lateral and medial frontal regions during the past and future tasks, as well as unique hippocampal connectivity with the dorsal attention network during the future task. It is possible that the additional neural resources recruited by the depression group, particularly during the future condition, may reflect greater effort given that the behavioral results from this fMRI study indicated that the deficit for specific events was significantly greater in the future than the past condition (Hach et al. 2014). That is, while the depression group generated significantly fewer specific future events than controls, this group difference was not significant for past events. Preliminary findings from a follow-up study we have conducted suggest that non-hippocampal

factors such as strategic retrieval abilities may also contribute to this differential deficit of future simulation in depression (Hach et al. 2013).

However, for both depression and healthy aging, fMRI studies that decompose the component processes of future simulation (i.e., access to episodic details, recombination, novelty and encoding) are yet to be conducted. Such studies would provide a fuller and more nuanced picture of the changes in hippocampal function across these different groups and different types of future simulation deficits.

Future Directions and Concluding Comments

The findings and ideas discussed in this chapter indicate clearly that much has been learned about the contributions of the hippocampus to episodic simulation. Although it is equally clear that much remains to be learned, given that research on this topic only began in earnest within the past decade, the rapid recent increase in relevant data and theorizing is impressive and suggests that interest and activity will only continue to increase during the coming years. We conclude by briefly considering a couple of possible directions for future studies.

A recurring theme running through this chapter centers on the importance of distinguishing among component processes that support episodic simulation. Thus we have focused processes such as relational encoding, novelty processing, detail retrieval and recombination, and also referred to related concepts such as scene construction, all of which are thought to rely on the hippocampus. But it is important to note that experimental paradigms used to assess episodic simulation may also be influenced by other factors that have not been linked specifically to hippocampal function. The point is well illustrated by behavioral studies from our laboratory focused on aging and episodic simulation. As noted earlier, in studies using the AI (Levine et al. 2002) we found that older adults reported fewer internal (episodic) details and more external (semantic) details than younger adults both when they remembered past experiences and imagined future experiences (Addis et al. 2008, 2010). We initially interpreted these findings as support for the constructive episodic simulation hypothesis—i.e., that age-related changes in episodic memory are responsible for reduced internal details in older adults during both remembering and imagining. However, a subsequent study from our laboratory (Gaesser et al. 2011) showed that when older adults were asked to describe a picture of a complex scene—a task that we assumed would not recruit episodic memory mechanisms—they also produced fewer internal details (i.e., details present in the picture) and more external details (i.e., commentary and inferences about the picture) than did younger adults. These findings suggest that changes in such non-episodic processes as narrative style or communicative goals that occur with aging (see, for example, Adams et al. 1997; Labouvie-Vief and Blanchard-Fields 1982) impact both memory and simulation tasks, and thus contribute to the observed similarities between memory and simulation as a function of aging.

They also raise the possibility that even in studies that are not focused on aging, similarities between remembering the past and imagining the future might reflect primarily the influence of general, non-episodic processes, such as communicative goals or narrative style. If this is the case, it could have implications for interpreting hippocampal activations during episodic simulation which, contrary to theoretical approaches such as the constructive episodic simulation hypothesis, might be related to these non-episodic processes.

To begin to address the issue, we have carried out a series of recent studies in our laboratory that have allowed us to distinguish the impact of general, non-episodic processes such as narrative style or communicative goals from processes more closely related to episodic retrieval. We have done so by using what we refer to as an *episodic specificity induction*: brief training in recollecting details of a recent experience (Madore et al. 2014; Madore and Schacter 2016; for review and discussion, see Schacter and Madore 2016). In these studies, participants receive either an episodic specificity induction, where they are guided to focus on retrieving specific details from a recently viewed video (i.e., details of people, objects, and actions), or a control induction, where they are guided to provide general impressions of a video (i.e., how much they liked it, how well made they thought it was). The critical finding from these studies is that after receiving the specificity induction, participants later provide more internal or episodic details, but not external or semantic details, on subsequent tasks that involve remembering the past or imagining the future than after receiving the control induction. By contrast, the specificity induction has had no impact on a picture description task (Madore et al. 2014) or another semantic task that requires providing definitions of words (Madore and Schacter 2016).

These findings indicate that a specificity induction can dissociate the contributions of episodic retrieval and closely related processes (e.g., event or scene construction; see Schacter and Madore 2016) on the one hand from more general narrative or semantic processes on the other. Linking back to the hippocampus, in light of these behavioral results we have hypothesized that after receiving a specificity induction, hippocampal activity should increase when participants are scanned as they perform an episodic simulation task. We have recently reported an fMRI study that indeed provides evidence for increased activity in the hippocampus and other core network regions during an episodic future simulation task after a specificity induction versus after a control induction (Madore et al. 2016).

These preliminary findings suggest that specificity inductions could prove to be useful tools in helping to pinpoint the processes supported by the hippocampus during episodic simulation. We have also shown that the specificity induction can impact related tasks, such as means-end problem solving (Madore and Schacter 2014) and divergent creative thinking (Madore et al. 2015), for which there is also evidence of hippocampal or medial temporal lobe involvement (e.g., for means-end problem solving see Sheldon et al. 2011; for divergent creative thinking, see Benedek et al. 2014; Duff et al. 2013).

Finally, we began by noting at the outset of the chapter that according to a recent taxonomy of prospection, four basic modes of future thinking can be distinguished

that vary along an episodic-semantic gradient: simulation, prediction, intention, and planning (Szpunar et al. 2014b). We have discussed only studies of episodic simulation in the current chapter because that has been the major focus on research related to the hippocampus in our lab and in other labs. But an intriguing question for future research concerns the extent and nature of hippocampal involvement in other forms of prospection. For example, there is an extensive literature from cognitive and social psychology concerning what is termed *episodic prediction* in our taxonomy, that is, estimating the likelihood of an outcome to a particular future autobiographical event or one's subjective response to that outcome. Studies of affective forecasting have shown that when making predictions about how they would feel in upcoming situations, people often overestimate or underestimate their future happiness (Gilbert and Wilson 2007). Gilbert and Wilson (2007) have linked these mistaken predictions to limitations on the kinds of episodic simulations that people construct regarding future scenarios, e.g., they have suggested that simulations sometimes capture the most salient but not the most likely elements of an experience, and at other times omit nonessential details that can impact future happiness. We are not aware of any evidence linking hippocampal activity to these kinds of episodic predictions, but given hippocampal involvement in episodic simulations, we expect that the hippocampus would also be involved in episodic predictions of future affective states.

Other modes of future thinking have received somewhat more attention in cognitive neuroscience research. For instance, studies of prospective memory have demonstrated a clear role for the hippocampus in encoding and retrieving delayed intentions for specific autobiographical events, or what we refer to as *episodic intentions* in our taxonomy (e.g., Cohen and O'Reilly 1996; Kliegel et al. 2008; Poppenk et al. 2010). Nonetheless, next to nothing is currently known about whether the hippocampus plays a similar role in processing intentions about non-specific autobiographical goals (e.g., forming an intention to become a better student; *hybrid intentions* in the taxonomy) or specific but non-autobiographical goals (e.g., setting a fiscal goal for a sales team; *semantic intentions*). Moreover, whether the hippocampus plays a role in processing delayed intentions beyond ensuring that those intentions are successfully encoded and retrieved remains to be elucidated in the literature.

Recent evidence also suggests a role for the hippocampus in episodic or autobiographical planning, which involves the organization of steps that need to be executed in order to attain a specific autobiographical future event or outcome. A series of studies conducted in our laboratory by Spreng and colleagues have used an autobiographical planning task in which participants are scanned while they mentally formulate plans to achieve specified goals. For example, a participant might be asked to formulate a plan to achieve the goal of academic success, and to integrate into the plan designated steps (attend class, study) and obstacles to be overcome (taking tests). Spreng et al. (2010) found that such autobiographical planning recruited all of the key regions within the core network discussed earlier including the hippocampus, and that activity within the core network during planning was coupled with activity in executive regions of the frontoparietal control network (see

also, Spreng and Schacter 2012; Spreng et al. 2013). More recent analyses indicate that hippocampal activity during autobiographical planning is associated with more detailed and specific autobiographical plans (Spreng et al. 2015).

It is interesting to note in relation to the foregoing studies that there have been numerous studies of maze learning and spatial navigation in rats that suggest that activity in hippocampal neurons can serve predictive and planning functions via a neural “preplay” of upcoming events that allow the rat to use past experiences to plan future actions (for review and discussion, see Buckner 2010; Wikenheiser and Redish 2015). Although the relation between these studies and research on human future thinking and imagination is not fully understood, the two lines of research converge in that they point toward an important prospective function for the hippocampus. We expect that during the coming years, studies of both humans and non-human animals will continue to provide novel insights into the contribution of the hippocampus to imagination, future thinking, and related forms of cognition.

Acknowledgements Preparation of this chapter was supported by National Institute of Mental Health Grant MH060941 and National Institute on Aging Grant AG08441 to DLS and Rutherford Discovery Fellowship (RDF-10-UOA-024) to DRA.

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