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The hippocampus and imagining the future: Where do we stand?

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Abstract

Recent neuroimaging work has demonstrated that the hippocampus is engaged when imagining the future, in some cases more than when remembering the past. It is possible that this hippocampal activation reflects recombining details into coherent scenarios and/or the encoding of these scenarios into memory for later use. However, inconsistent findings have emerged from recent studies of future simulation in patients with memory loss and hippocampal damage. Thus, it remains an open question as to whether the hippocampus is necessary for future simulation. In this review, we consider the findings from patient studies and the neuroimaging literature with respect to a new framework that highlights three component processes of simulation: accessing episodic details, recombining details, and encoding simulations. We attempt to reconcile these discrepancies between neuroimaging and patient studies by suggesting that different component processes of future simulation may be differentially affected by hippocampal damage.

1. Introduction

In daily life, particularly during the unoccupied moments, we often revert to our inner mental world and engage with our aspects of our lives outside of the present. Mentally projecting ourselves back into the past or forwards into the future can take make forms – a cursory thought, a vague image, or a vivid and consuming scenario. There has been increasing interest in understanding the ways in which remembering and future thinking are similar or different, both in terms of cognitive and neural processes, and whether such characteristics are evident for various forms of past and future thinking (for recent reviews, see Schacter, Addis, & Buckner, 2008; Szpunar, 2010). These studies have been informed by a closely related line of neuroimaging research showing that when people are consumed by various forms of thoughts and images, these internally-directed cognitive activities are accompanied by a characteristic pattern of neural activity - known as the default network (Buckner, Andrews-Hanna, & Schacter, 2008; Spreng, Mar, & Kim, 2009).

This network, which includes many regions traditionally associated with memory, such as the hippocampus, is also up-regulated by tasks that specifically require a focus on remembering and imagining personal experiences (Buckner & Carroll, 2007; Schacter, Addis, & Buckner, 2007; Spreng et al., 2009). Motivated by findings that remembering and imagining engage the same 'common core network', we advanced the *constructive episodic simulation hypothesis*, which holds that the common neural activity for past and future reflects a reliance on memory to provide the details comprising both remembered and imagined event representations (Schacter & Addis, 2007). In that theory, as well as in this review, we focus on a particularly vivid form of future thinking: the imaginative construction or simulation of scenarios that might occur in one's future. We hypothesized that the flexible use of episodic details from memory during imaginative simulations of the future can help to understand constructive aspects of memory, such as its susceptibility to distortion (see also Schacter, Guerin, & St. Jacques, 2011). Like autobiographical memories of past experiences, these simulations are considered "episodic" in nature because they represent the self engaging in a specific event in a particular spatiotemporal context. And although the emphasis here is primarily on simulations located in the imagined future, primarily because of the adaptive value of such simulations for maximizing future success (Ingvar, 1985; Schacter & Addis, 2007; Suddendorf & Corballis, 1997, 2007; Szpunar, 2010), simulations can also focus on present or past events; indeed, we have argued that many of the same processes discussed here are likely also applicable under those conditions (Addis, Pan, Vu, Laiser, & Schacter, 2009).

One of the more compelling and even unexpected findings from research on the neural underpinnings of episodic simulations is that the hippocampus, a region traditionally thought of as a "memory region", can be engaged to a greater degree when imagining than remembering (e.g., Addis, Wong, & Schacter, 2007; for reviews, see Buckner, 2010; Schacter & Addis, 2009). Such findings raise the question of what is unique about episodic simulation or future thinking that recruits the hippocampus. In very general terms, it would appear that more intensive processing is required when imagining future events relative to retrieving past events, because the former requires construction of a novel event, whereas the latter involves retrieval of an already established event. However, determining what specific component processes underlie this 'more intensive processing', and which such processes rely on the hippocampus, is necessary to better understand this future>past effect. A number of candidate cognitive processes exist. Although both remembering and imagining typically involve the reactivation of memories and episodic details comprising these memories, only imagining requires the additional step of recombining such details into a new arrangement – the imagined scenario. It is plausible that this recombination process would engage the hippocampus, given its role in relational memory processes that link together disparate bits of information (Eichenbaum, 2001). Also, if these newly constructed scenarios are ever to be accessed in future, they need to be encoded and stored in memory (Ingvar, 1985). In this review, we will discuss the conditions under which a hippocampal future>past effect emerges, and also consider recent work investigating whether hippocampal activation during future thinking reflects access to episodic details, recombining these details to construct specific scenarios, and/or the encoding of these scenarios into memory.

A related line of enquiry is to determine not only whether the hippocampus is active during future simulation but whether it makes a critical and necessary contribution. While it has been long established that a functioning hippocampus is necessary for the retrieval of detailed autobiographical memories (for a review, see Moscovitch et al., 2005), it is less clear whether this is the case for future simulation (see Table 1 for a summary of patient cases discussed herein). While some patients with hippocampal damage and impaired episodic memory also exhibit difficulties in imagining detailed and coherent future events (Andelman, Hoofien, Goldberg, Aizenstein, & Neufeld, 2010; Hassabis, Kumaran, Vann, & Maguire, 2007; Race, Keane, & Verfaellie, 2011), other studies do not report imagination deficits in such patients. Spared simulation abilities in the context of hippocampal damage and memory loss have been reported in an adult developmental amnesic patient (Maguire, Vargha-Khadem, & Hassabis, 2010), a group of developmental amnesic school-aged children (Cooper, Vargha-Khadem, Gadian, & Maguire, 2011; see also, Hurley, Maguire, & Vargha-Khadem, in press), and a group of adult patients with bilateral hippocampal damage (Squire et al., 2010).

--Insert Table 1 about here--

Such findings imply that a fully intact hippocampus may not be required for future simulation. However, the inconsistent results yielded from these studies raise a number of important questions. Does the temporal extent of amnesia influence the degree to which imagined scenarios can be constructed? Does the age of onset of hippocampal damage affect the degree of impairment? Does the location of the damage within the hippocampus influence the pattern of spared and impaired abilities? Can residual hippocampal tissue support future simulation? Are particular simulation tasks better able to detect deficits? In considering the findings from patient studies in conjunction with those from neuroimaging literature, we will attempt to reconcile these discrepant results by suggesting that different component processes of future simulation may be differentially affected by hippocampal damage: although the processes of accessing and recombining details to construct and encode a future event are inherently related processes in healthy individuals, it is possible that in the damaged brain these processes are, to some extent, dissociable.

2. Access to memory details: the episodic fodder for future simulations

In recent years, neuroimaging has provided evidence to suggest that imagining the future relies on much of the same neural machinery as remembering the past. One hypothesis that such findings motivate is that memories must be reactivated in order to extract the information needed to ‘flesh out’ detailed simulations. Indeed, if simulations involve the projection of the self in time beyond the present (Buckner & Carroll, 2007) and are to be meaningful for that individual, then personally-relevant episodic details from memory are needed. Such elements would include the major components of an episode, including the people, places and objects previously encountered by the individual. In their scene construction hypothesis, Hassabis and Maguire (2007) argue that spatial information is particularly important. A spatial framework provides a platform upon which to build the scenario, and without this, an imagined event would likely lack a sense of coherence.

Although common hippocampal activity for past and future events is suggestive of access to mnemonic information during both tasks, it is not conclusive. Addis and Schacter (2008) examined whether hippocampal responses during remembering and imagining were modulated by subjective ratings of the detail comprising these events. Activity in the posterior hippocampus correlated with detail ratings for both past and future events, consistent with the idea that both tasks require access to episodic details. Moreover, Weiler, Suchan and Daum (2010b) found activity in the posterior hippocampus was associated with both past and future events, though the responses had differing timecourses. Nevertheless, the location of this neural response dovetails with studies implicating the posterior hippocampus in retrieval as opposed to encoding (Lepage, Habib, & Tulving, 1998; Prince, Daselaar, & Cabeza, 2005; Schacter & Wagner, 1999), in the reinstatement of previous conditions (Giovanello, Schnyer, & Verfaellie, 2009; Preston, Shrager, Dudukovic, & Gabrieli, 2004), and in the amount of detail comprising autobiographical memory (Addis, Moscovitch, Crawley, & McAndrews, 2004).

However, the most convincing evidence that access to episodic details may be *necessary* for future simulations comes from studies of patients with memory loss (see Table 1). One of the early observations of a link between past and future thinking came from Tulving (1985). In a discussion of K.C., a patient with dense autobiographical amnesia resulting from a head injury, it was also noted that K.C. exhibited difficulties in imagining specific episodes in his personal future. Similarly, amnesic patient D.B., who sustained brain damage as a result of cardiac arrest and anoxia, cannot remember or imagine personal events (Klein, Loftus, & Kihlstrom, 2002). In both cases, the neuroanatomical damage is not restricted to the hippocampus (patient KC has damage in and beyond the hippocampus, including extensive prefrontal damage, Rosenbaum et al., 2005; no neuroanatomical findings have been reported for patient D.B.). Nevertheless, these reports raised the possibility that there is a link between remembering and imagining – that being able to access details from episodic memory may be an important and perhaps necessary condition of the successful construction of episodic simulations.

Similar results have been reported in patients with damage reported to be limited to the hippocampus. Hassabis et al. (2007) found that four out of five patients with hippocampal amnesia could not construct imaginary scenarios of everyday scenes: their constructions contained significantly less content that those of controls, and the details that were generated were not well integrated. Although the authors also found that providing patients with details did not improve their performance, the provided information was semantic in nature and therefore may not have been sufficient to support imaginings that have an episodic basis. One critical issue is whether these patients have damage circumscribed to the hippocampus. Although Maguire and Hassabis (2011) state these patients were "specifically selected" for damaged restricted to the hippocampus, Squire and colleagues (Squire, McDuff, & Frascino, 2011) disagree with this assessment. They argue that aspects of the clinical profiles of these patients (e.g., generalized atrophy, seizures, personality change) suggest the presence of damage outside of the hippocampus. They also note that the one patient in the Hassabis et al. (2007) study who did not exhibit imagination deficits had a different etiology (meningeoencephalitis and recurrent meningitis, versus limbic encephalitis in the four other patients), as well as residual hippocampal tissue and function (Hassabis et al., 2007).

Race and colleagues (2011) examined the ability to remember and imagine in a group of eight amnesic patients with medial temporal damage. This study is important for two reasons. First, the paradigm included a condition in which participants were required to construct narratives when the details did not have to be retrieved from memory but were presented as pictures (also see Gaesser, Sacchetti, Addis, & Schacter, 2011). When completing the past and future tasks, amnesic patients generated significantly fewer episodic details than did controls, and the number of episodic details for past and future narratives was correlated. Critically, hippocampal damage did not disrupt the ability to construct a narrative in the picture condition, where access to episodic memory was not required. Moreover, performance on the picture narrative task was not correlated with performance on the future task. Second, although the etiology and extent of damage varied across the eight patients, there was one patient in whom damage was confirmed as being limited to the hippocampus. Importantly, the performance of this patient mirrored that of the other patients who had some degree of extra-hippocampal temporal damage, suggesting that damage to the hippocampus alone is sufficient to disrupt future simulation. Together, the observations from this study further support the notion that in the context of hippocampal damage, it is an inability to access details in episodic memory, and not more general deficits in narrative ability, that underlies deficient episodic simulation performance.

While studies of amnesia give insight into the ability to simulate when there is little, or no, access to episodic details, studies of aging -- where deficits in accessing past events are present but comparatively milder -- have also provided relevant evidence. In a series of studies, we have examined the ability to remember and imagine in healthy and also in pathological aging (i.e., patients in the early stages of Alzheimer's disease), in which autobiographical memory is typically affected (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002), and hippocampal atrophy and dysfunction are also evident (Hedden & Gabrieli, 2004). In these studies, we had participants generate memories of past events and simulations of future events in response to word cues and found that the number of episodic details comprising events in older or demented adults was reduced relative to appropriate control groups (for a review, see Schacter, Gaesser, & Addis, 2010). Moreover, the number of episodic details for past events is strongly correlated with the number of details comprising future events. These correlations are consistently evident across old and young (Addis, Musicaro, Pan, & Schacter, 2010; Addis, Wong, & Schacter, 2008), and across demented and healthy older adults (Addis, Sacchetti, Ally, Budson, & Schacter, 2009), and exist even when controlling other factors that may more generally influence the detail of narratives, such as cognitive decline and verbal fluency (Addis, Sacchetti, et al., 2009). The deficits in episodic remembering and imagining that we have documented in older adults do also extend to a picture description task that does not require episodic memory (Gaesser et al., 2011). Nonetheless, we also found that the age deficits in remembering and imagining were still observed after controlling for general narrative abilities, as measured by this picture description task. Neuroimaging evidence suggests that the reduction in episodic detail when older adults describe past and future events may be related to dysfunction in the regions supporting episodic detail, including the hippocampus (Addis, Roberts, & Schacter, 2011).

What is to be made, then, of patients with memory loss who can still imagine the future? Such findings appear to speak against the idea that access to memories is a critical precursor to future simulation. As noted earlier, Squire et al. (2010) reported that a group of patients with damage to the hippocampus showed an intact ability to create detailed imaginary future events. However, although these patients have hippocampal damage, it is notable that their degree of retrograde amnesia is minimal: these patients can retrieve events from the remote past, and only exhibit a mild (and non-significant) deficit for retrieving memories from the recent past. Thus, the results of this study could also be interpreted as supporting the notion that access to the past – even in the context of hippocampal damage – can provide a basis for imagining the future.

However, there are reported cases of hippocampal damage that has differentially affected remembering but not imagining. For instance, Maguire and colleagues reported that developmentally amnesic patients who sustained hippocampal damage early in life can construct imaginary scenarios (Maguire et al., 2010; Hurley et al., in press; but see, Kwan, Carson, Addis, & Rosenbaum, 2010). Moreover, as noted earlier, one of the patients from the Hassabis et al. (2007) study could also complete their scene construction task. Interestingly, some of these patients have been noted to have residual hippocampal tissue that appears to be functional, in that it is activated during memory tasks (Maguire et al., 2010), although such activation has not yet been shown during future simulation. These researchers also report normal imagination abilities in a group of children with hippocampal damage and amnesia (Cooper et al., 2011), further suggesting that the time of onset of the amnesia may be an important consideration. It is possible that with early damage, these patients develop other strategies or rely either on residual episodic memories or detailed semantic information to construct scenarios (Cooper et al., 2011).

It is also notable that these findings have emerged using the scene construction task. Hassabis et al. (2007) mention that this task was designed to "increase the dependence of constructions on generalized semantic memory representations". On each trial, a sentence cue (e.g., "Imagine you are lying on a white sandy beach") is provided to take participants into a generic scene; it is very likely that this scene can then be fleshed out with semantic detail. Thus, it is possible that these patients are able to complete this particular imagination task using detailed yet semantic representations of how certain scenes or episodes unfold, rather than extracting information from their own experiences. However, when the task requires creation of a specific and novel episode, similar patients (e.g., with developmental amnesia) show simulation deficits – particularly in the amount of episodic detail generated (Kwan et al., 2010). Although amnesics may generate fewer episodic details relative to controls, they sometimes show little or no reduction in the number of semantic details comprising their event narratives (Race et al., 2011). It has also been shown in other studies that patients with episodic, but not semantic, memory deficits can successfully complete future thinking tasks that are based primarily on general knowledge (e.g., non-personal future tasks; Klein et al., 2002).

When faced with reduced or no access to episodic memory, it may be a natural compensation strategy to rely on semantic information to aid in describing autobiographical events. Using a scoring technique that specifically parses episodic from non-episodic information (Levine et al., 2002), we have also found that although older adults show a decline in the amount of episodic detail comprising their past and future events, they show a corresponding increase in the amount of non-episodic, conceptual information (Addis et al., 2010; Addis et al., 2008; note also that this pattern extends to picture description; Gaesser et al., 2011). In line with this finding, older adults also show an increase, relative to young, in their recruitment of lateral temporal regions during autobiographical tasks (Addis et al., in revision); these regions are thought to mediate semantic and conceptual autobiographical information (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004; Graham, Lee, Brett, & Patterson, 2003).

Another key question is whether access to episodic details is *sufficient* for future simulation to occur. It is likely that this ability is only a starting point; once episodic details are extracted, they still have to be used in a meaningful way, which we have argued requires additional processes such as detail recombination (e.g., Addis & Schacter, 2008; Schacter & Addis, 2009). Nonetheless, the findings discussed earlier of intact future simulation performance in hippocampal amnesics with relatively preserved autobiographical memories (Squire et al., 2010) suggests that access to episodic details may be sufficient for future simulation. By contrast, Andelman et al. (2010) reported a case study of a patient, M.C., with a bilateral hippocampal lesion and loss of autobiographical memory restricted only to the past 3 years. Thus, at 27 years of age, she still had approximately 20 years of episodic memories to draw upon when completing a future simulation task. M.C. was, however, unable to do so: when asked to describe her personal future, her responses were vague and general, or she reported that she simply didn't know. Because there was no quantitative assessment of future simulation performance in this case, the results must be interpreted cautiously. Still, they raise the possibility that while access to episodic details may be necessary in order to construct episodic simulations, it may not be sufficient.

3. Detail recombination: constructing a coherent scenario

As we have reviewed above, being able to access details from episodic memory can be conceptualized as an initial stage in the process of episodic simulation. Of course, having a jumble of details is useless if they cannot be recombined and integrated appropriately. We have argued that 'detail recombination' is critical to imagining coherent scenarios – the kinds of simulations one creates when thinking about experiences relevant in their daily lives. Given the role of the hippocampus, particularly the anterior hippocampus, in relational processing, we have argued that this region is likely critical in the ability to form coherent scenarios (e.g., Addis & Schacter, 2008; Schacter & Addis, 2009).

This proposal is based on an integration of findings from various neuroimaging studies. An early meta-analysis of medial temporal activity during memory tasks reported that the anterior portion of the hippocampus appears to be particularly responsive to tasks with relational demands (Schacter & Wagner, 1999); subsequent work has further supported this anterior localization of relational memory processes (e.g., Chua, Schacter, Rand-Giovannetti, & Sperling, 2007; Giovanello, Schnyer, & Verfaellie, 2004; Jackson & Schacter, 2004; Kirwan & Stark, 2004; Staresina & Davachi, 2008, 2009). The role of this region within the realm of relational memory may be further refined, based on findings from Preston et al. (2004; see also Heckers, Zalesak, Weiss, Ditman, & Titone, 2004). This work suggests that the anterior hippocampus may be particularly involved in the recombination of details extracted from various memories. Using a transitive inference paradigm, participants first learned to associate one set of items (faces, A) with another set of items (houses, B). They then learned to associate those same houses (B) with a new set of items (novel faces, C).

During the scanning session, seeing items (A, B, or C) taken from any of the memories (A-B, B-C) resulted in posterior hippocampal activity, further implicating the posterior hippocampus in retrieval or reinstatement. However, seeing novel rearrangements of such details (A-C) resulted in selective anterior hippocampal activity. This recombination process can be considered analogous to future simulation, where we argue details extracted from different memories that may have not been encountered together in reality, are rearranged in imagination – and similarly, this recombination process should also engage the anterior hippocampus.

More recently, Staresina and Davachi (2009) investigated hippocampal responses to the process of integrating details across time and space. They identified a region in the anterior hippocampus that was more responsive when details were presented in a spatiotemporally discontiguous manner (i.e., separated across time and space) and required integration, relative to when details were presented in a contiguous, integrated form. Conceptually, we suggest that this process again maps onto the kind of recombination thought to occur during simulation: an integration of details from memories formed in different spatiotemporal contexts.

The findings of Preston et al. (2004) and Staresina and Davachi (2009) dovetail with those from a neuroimaging study of past and future detail. In that study, we (Addis & Schacter, 2008) found common responses to detail of past and future events in posterior hippocampus, but the anterior hippocampus was responsive only to the amount of detail comprising future events – which are presumably recombined across spatiotemporally distinct experiences. Interestingly, we have replicated the finding of differential future activity within the anterior hippocampus across a number of studies using autobiographical cuing (e.g., Addis, Wong, et al., 2007; adapted from Crovitz & Schiffman, 1974) and experimental recombination paradigms (Addis, Pan, et al., 2009). While the cueing task requires an individual to generate future events from generic cues (nouns), the experimental recombination paradigm uses random rearrangements of episodic details (persons, places, objects) taken from the individual's own memories, thus ensuring that detail recombination occurs. Moreover, these paradigms enable examination of activity during the initial construction of the future event when the cue is presented, and the subsequent elaboration of the event once it is in mind. With this approach, we have found that over the course of a simulation trial, this activity typically emerges during the initial construction phase rather than being evident throughout the duration of a simulation trial (Addis, Cheng, Roberts, & Schacter, 2011; Addis, Pan, et al., 2009; Addis, Wong, et al., 2007; Martin, Schacter, Corballis, & Addis, 2011). This temporal pattern suggests that the differential future-related activity is associated with processes occurring early in the construction of future events, when detail recombination would be expected to occur. Other labs have also reported similar future>past effects in the anterior hippocampus. For instance, Weiler and colleagues (Weiler, Suchan, & Daum, 2010a) found that imagining future events that had a low probability of occurring during the upcoming holidays was associated with more anterior hippocampal activity than events with a higher probability of occurring. The authors suggested that perhaps low probability events place a higher demand on the binding of disparate event features relative to high probability events that may be already planned.

Determining the boundary conditions of the future>past effect will provide a better understanding of whether detail recombination is important for engaging the anterior aspect of the hippocampus. Importantly, we have recently shown that this effect is limited to certain types of future events. We examined hippocampal activity when imagining specific (unique) and general (routine) future events, hypothesizing that constructing a specific future event should place greater demand on recombining details and hippocampal resources relative to constructing a generic future event that more closely relies on conceptual knowledge about routines (Addis et al., 2011). Indeed, our analysis supported this hypothesis, demonstrating that hippocampal activity was strongest when imagining specific future events relative to more generic and routinized ones. Participant ratings confirmed that specific future events were more detailed and novel than general future events, further suggesting that the process of constructing an event that is both detailed *and* novel engages the anterior hippocampal region. Additionally, because these findings suggest that the hippocampus is not strongly engaged by constructing generic future events, it may not be surprising that patients with hippocampal damage can imagine the future in a gist-like, conceptual manner.

These observations from neuroimaging studies suggest that dysfunction in the hippocampus may result in deficits in recombining details. Several findings suggest the presence of such difficulties. Hassabis et al. (2007) found that not only did the events constructed by hippocampal amnesics lack content overall, but the details they did generate were not well integrated and lacked a spatial coherence. In healthy older adults who show some degree of structural and functional dysfunction in the hippocampus (Hedden & Gabrieli, 2004), we found that the integration of memory details into simulations was reduced relative to young adults (Addis et al., 2010). Using the experimental recombination paradigm, we experimentally ‘extracted’ person, place and object details from different past events; random recombinations of a participant’s memory details were later presented during a future simulation task. Importantly, each future simulation was required to include the person, place and object details presented. While both groups were able to include all three details in the simulations, the young group was better able to integrate these three details into the same imagined spatiotemporal context. In contrast, older adults integrated on average two of the three details into the same spatiotemporal context, and then often touched on the third detail in a separate context, essentially resulting in a series of ‘mini-events’. These findings suggests that even with experimental support to access details from various episodic memories, the ability to integrate these details into a coherent scenario with a specific temporal and spatial context may be reduced in populations with compromised hippocampal function.

Again, one might raise the question that if the hippocampus is necessary for detail recombination, how is it that some patients with hippocampal damage can imagine seemingly coherent future events? One issue is that not every study of future simulation in patients includes a measure of detail integration or spatial coherence and thus in instances where hippocampal patients can successfully imagine, it can be difficult to determine whether the scenarios constructed were in fact coherent. Maguire and Hassabis (2011) argue that the number of spatial references produced by the patients studied by Squire et al. (2010) appear reduced relative to the typical level of controls, suggesting that these patients may have been creating primarily semantic representations. Moreover, it is possible to imagine a future event with minimal, if any, detail recombination: one can “recast” past events into the future. It is possible that paradigms using single cues may elicit recasting. For instance, if shown the cue word “car”, one might recall a relevant experience (“my car breaking down and my husband picking me up”) and then imagine that experience unfolding in the same way in future. In many protocols, it is ensured that participants are generated novel scenarios (e.g., Addis, Wong, et al., 2007, 2008; Hassabis et al., 2007), but this is not always done or reported. In order to circumvent this possibility, we designed an experimental recombination paradigm in which participants are required to recombine details extracted from their own past events (Addis et al., 2009). Although this paradigm has been employed with older adults (Addis et al., 2010), replicating our findings using the cue word paradigm, it has not yet been used to assess recombination abilities in patients with circumscribed hippocampal damage. The results of such a study would be of considerable interest.

4. Memory for the future: encoding future simulations

Differential engagement of the anterior hippocampus may also reflect the process of encoding newly-imagined scenarios. Indeed, the anterior portion of the hippocampus has been implicated in encoding (Schacter & Wagner, 1999; Spaniol et al., 2009), particularly for relational (e.g., Chua et al., 2007; Jackson & Schacter, 2004; Kirwan & Stark, 2004; Staresina & Davachi, 2008, 2009) and novel (Kohler, Danckert, Gati, & Menon, 2005) information. If the adaptive significance of simulating several alternative "behavioral modes" is to maximize success in anticipated situations (Ingvar, 1985) and flexible planning (Boyer, 2008), then retaining this "fitness-relevant" information in memory for future reference is a necessary step. Nairne, Thompson and Pandeirada (2007) investigated whether information relevant to survival is remembered better than survival-irrelevant information. In that study, participants judged whether items were relevant to survival (having provisions and protection) or moving (moving to a foreign country) situations, or judged the items for pleasantness. In line with the idea that we are tuned to remember fitness-relevant information, subsequent memory performance was boosted for items rated as survival-relevant. Interestingly, more recent work using a variant of the paradigm developed by Nairne and colleagues suggests that the much of the benefit of "survival processing" may be attributable to the engagement of encoding processes that support planning for the future (Klein, Robertson, & Delton, 2010).

Three kinds of evidence demonstrate the adaptive value of simulations. First, it is well established that simulations play an important role in psychological well-being. Being able to generate specific and detailed simulations of future events can enhance one's ability to cope with upcoming situations (Brown, MacLeod, Tata, & Goddard, 2002; Taylor, Pham, Rivkin, & Armor, 1998; Taylor & Schneider, 1989). For instance, creating simulations about positive future outcomes can improve emotion regulation, resulting in decreased amounts of worry related to upcoming future events (Brown et al., 2002). In addition to helping one cope with the prospect of an upcoming event, mentally simulating appropriate actions for future stressful situations can enhance one's ability to cope if and when those situations arise (Taylor & Schneider, 1989).

Second, simulations are used when attempting to solve open-ended or ill-defined problems, where different possible solution paths need to be mentally evaluated. Using the Means-Ends Problem Solving Test, Sheldon and colleagues (Sheldon, McAndrews, & Moscovitch, 2011) examined the ability of older adults and patients with temporal lobe epilepsy to solve open-ended social problems. Both of these groups are known to have some degree of impairment on tasks of autobiographical memory (Addis, Moscovitch, & McAndrews, 2007; Levine et al., 2002; St-Laurent, Moscovitch, Levine, & McAndrews, 2009); older adults are also known to show reduced performance on episodic simulation tasks (Addis et al., 2008). It was found that when simulating solutions to ill-defined problems, both groups generated fewer relevant steps than controls. This finding suggests that without full access to episodic memory and the ability to generate detailed simulations, the effectiveness of problem solving is reduced (for relevant neuroimaging evidence, see Gerlach, Spreng, Gilmore, & Schacter, 2011; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010).

Third, recent studies have demonstrated that episodic simulation has a significant impact on temporal discounting of future rewards: when people imagine experiencing a reward in the future, they show an increased tendency to favor rewards that produce greater long-term payoffs, thereby countering the normal tendency to devalue delayed rewards (Benoit, Gilbert, & Burgress, 2011; Peters & Büchel, 2010). Interestingly, fMRI data reveal that these effects of episodic simulation on temporal discounting are associated with increased coupling between activity in the hippocampus and prefrontal regions involved in reward representation (Benoit et al., 2011; Peters & Büchel, 2010). Related studies have shown that varying the manner in which memory is queried can also influence temporal discounting toward long-term payoffs when memory queries emphasize the production of patient (vs. impatient) thoughts (Weber et al., 2007). It would be interesting to approach effects of episodic simulation on temporal discounting from the theoretical perspective of query theory (Johnson, Haubl, & Keinan, 2007) and to determine whether the memory-based effects on temporal discounting have a similar neural basis to those shown for episodic simulation.

In order to influence future behaviors and realize these adaptive benefits of simulation, it is important that simulations are encoded and maintained in memory (Ingvar, 1985; Szpunar, Addis, & Schacter, in press). There is indirect evidence to support this idea. For instance, individuals tend to act in a way that is consistent with or constrained by how they have imagined themselves in those situations (Johnson & Sherman, 1990), implying that some record of that simulation influences later behavior. There is typically a high correspondence of stated intentions and subsequent behavior (Fishbein & Ajzen, 1980). Consider also prospective memory, where an intention is encoded into memory and later accessed and implemented when triggered by a target event or time cue. It is likely that the intentions involved in prospective memory range in the degree to which they draw upon simulations. Particularly relevant to the idea of episodic simulation is the process of forming "implementation intentions" (Gollwitzer, 1999) which involve imagining and rehearsing a plan with reference to the specific future context in which it will be executed. Research has shown that creating implementation intentions significantly increases the likelihood of carrying out that intention (Chasteen, Park, & Schwarz, 2001; Orbell, Hodgkins, & Sheeran, 1997), again suggesting that these simulations are not only stored in memory but do influence future behavior. Poppenk and colleagues (Poppenk, Moscovitch, McIntosh, Ozcelik, & Craik, 2010) directly investigated the process of encoding intentions, using fMRI to see whether later memory for intentions was associated with hippocampal activity during encoding. They found that successful encoding of intentions engaged the hippocampus, as did the encoding of other forms of information, such as present actions. But unique to the prospective task was the recruitment of frontopolar cortex, consistent with finding that damage to this region results in deficits of prospective memory (e.g., Burgess, Veitch, de Lacy Costello, & Shallice, 2000).

If the involvement of the hippocampus in future simulation is only to encode imagined scenarios, then hippocampal damage would not necessarily result in an inability to construct simulations – just an inability to encode and retain them. There are some data to suggest that this might be the case (see Table 1). For instance, although children with hippocampal damage can imagine scenarios, when asked to recall them the following day, they do so with less accuracy and consistency than healthy controls (Cooper et al., 2011). Additionally, adults with hippocampal damage appear to repeat themselves more than controls when describing future events, possibly indicative of a failure to sufficiently encode the scenario as it is constructed (Squire et al., 2010).

We conducted an fMRI study (Martin et al., 2011) to investigate whether hippocampal activity during future simulation is indeed related to successful encoding by incorporating the experimental recombination (Addis, Pan, et al., 2009) and subsequent memory (e.g., Wagner et al., 1998) paradigms. During scanning, participants were presented with random recombinations of person, location, and object details taken from their own memories and for each set of details, they imagined a novel future event involving all three details. After scanning, participants completed an unexpected cued recall test, in which they were showed two details and had to recall the third. By this design, we had an objective measure of whether the critical details comprising each simulation were successfully encoded. As predicted, successfully encoded simulations were associated with greater activity in the anterior right hippocampus than simulations that were later forgotten. Moreover, the posterior right hippocampus was also modulated by encoding success. A functional connectivity analysis revealed that both the anterior and posterior hippocampus exhibited connectivity with each other and a wider brain network (including medial prefrontal and medial parietal regions) during successful encoding. When encoding was not successful, the posterior hippocampus did not show this pattern of connectivity. However, it is interesting to note that during unsuccessful encoding, the anterior region still exhibited connectivity with the wider core network. It is possible that this neural pattern reflects the attempt to construct a simulation, even if it is ultimately not encoded sufficiently to be recalled later. We also found that the imagined events that were later-remembered were on average more detailed that later-forgotten ones, and activity in regions exhibiting an encoding effect was also modulated by the level of detail. Together, these observations suggest that constructing a memorable scenario may be related, at least in part, to how well the composite details were retrieved from memory and recombined.

5. Future directions: mapping component processes to hippocampal regions

Considering together the patient and neuroimaging data reviewed here, there appears to be evidence supporting the idea that there are three important component processes involved in the simulation of episodic future events. First, details stored in episodic memory with which to furnish the simulation must be accessed. Second, the details extracted from various memories need to be recombined and integrated into a spatiotemporal context in order imbue a simulation with a sense of coherence. Third, if a simulation is to influence and guide future behaviours, it needs to be successfully encoded into memory. The evidence reviewed herein suggests that these different processes all rely, to some extent, on the hippocampus. It remains an open and important question as to whether different subregions of the hippocampus are specifically associated with specific component processes. While the posterior hippocampus likely supports the retrieval of previously experienced details, particularly those spatial in nature, the anterior hippocampus supports the recombination of extracted details into a coherent scenario, and both regions support successful encoding.

This framework may be able to inform the debate on whether hippocampal damage disrupts the ability to imagine the future (Maguire & Hassabis, 2011; Squire et al., 2010). It is critical that future research on patients with hippocampal damage employ more refined experimental designs to probe whether detail access, detail recombination and/or encoding of simulations is disrupted. The case study approach may particularly important here. There is considerable variance of performance across patients with hippocampal damage, and it will be important to understand the specific patterns of spared and impaired sub-processes within each case. Moreover, it is likely that the nature and location of damage to the hippocampus is critical. Differential impairments of the construction and/or encoding of future simulations may emerge depending on the nature of the hippocampal damage: whether it is confined to the anterior and/or posterior aspects, affects primarily the right hippocampus, affects the entirety of the structure, or extends beyond its boundaries. Moreover, it will be critical in future studies to ascertain whether damage in amnesic patients is restricted to the hippocampus or extends more broadly.

Another challenge will be to find ways in which to differentiate the process of recombining details to construct a simulation and the encoding of those simulations. These processes are closely related in two ways: cognitively, with more detailed simulations being more successfully encoded; and neurally, with both processes engaging the anterior right hippocampus. As such, they may be difficult to disentangle. One fruitful avenue may be to investigate whether detail recombination and successful encoding are mediated by specific hippocampal subfields. The hippocampal formation is a circuit comprised of several anatomically-distinct subregions, including the dentate gyrus, three cornu ammonis ($CA_1/CA_2/CA_3$) areas, and the subiculum. Recent work suggests a functional distinction between the input structures into the hippocampus (dentate gyrus/CA_2/CA_3) and the output (subiculum/CA_1). Specifically, while the input structures appear to be involved in encoding, the output structures may be more involved in binding (Carr, Rissman, & Wagner, 2010). Moreover, the finding that the dentate gyrus is involved in encoding is consistent with the hypothesis that the ability to form temporal associations among new experiences that happen close together in time is ultimately dependent upon the continuous production of new-born granule cells in the dentate gyrus (Aimone, Wiles, & Gage, 2006; Deng, Aimone, & Gage, 2010). Extrapolating these findings to the realm of future simulation, it is possible that detail recombination during future simulation may be differentially associated with CA_1/subiculum, and successful encoding with dentate gyrus/CA_2/CA_3. Recent developments in ultra-high-field 7T MRI to obtain exceptionally high resolution images of hippocampal subfield anatomy – including distinct layers within subfields (e.g. Kerchner et al., 2010) – will no doubt facilitate more detailed investigations of the roles of different hippocampal subfields.

Neuroimaging studies to date suggest there may also be lateralization effects in the hippocampal activity that is differentially associated with future thinking. Specifically, we initially reported that hippocampal activity common to past and future events was evident in the left hippocampus, but that the future>past effect was specific to the right hippocampus (Addis, Wong, et al., 2007). A number of other studies finding future-related activity also report a right lateralization (Addis et al., 2011; Martin et al., 2011; Weiler et al., 2010a, 2010b), although some studies report such activity is bilateral (Addis, Pan, et al., 2009). Interestingly, a patient with damage that affected only the right hippocampus exhibited difficulties in generating detailed future simulations (Race et al., 2011), suggesting the right hippocampus may indeed be critical to this ability. However, it remains to be determined what specific contribution the right hippocampus might be making to future simulation.

The research considered here is in an early stage of development. It is only during the past few years that studies examining the contribution of the hippocampus to imagining the future have begun in earnest, and it is clear that much remains to be learned. Further integration of this new line of work with more firmly established research on hippocampal contributions to memory encoding and retrieval will be critical to advancing our understanding, as will integration with animal studies of such related phenomena as prospective coding in the hippocampus (e.g., Ferbinteanu & Shapiro, 2003; Foster & Wilson, 2006; Johnson & Redish, 2007; for discussion, see Buckner, 2010). We are hopeful that these kinds of studies will help to increase our understanding of the neural and cognitive processes that link memory and imagination, and in so doing, provide new insights into how the future depends on the past.

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