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MEDIAL TEMPORAL LOBE CONTRIBUTIONS TO FUTURE THINKING: EVIDENCE FROM NEUROIMAGING AND AMNESIA

Mieke Verfaellie[(1)], Elizabeth Race[(1)], & Margaret M. Keane[(1,2)]*
(1) VA Boston Healthcare System and Boston University School of Medicine, USA, & (2) Wellesley College, USA

Following early amnesic case reports, there is now considerable evidence suggesting a link between remembering the past and envisioning the future. This link is evident in the overlap in neural substrates as well as cognitive processes involved in both kinds of tasks. While constructing a future narrative requires multiple processes, neuroimaging and lesion data converge on a critical role for the medial temporal lobes (MTL) in retrieving and recombining details from memory in the service of novel simulations. Deficient detail retrieval and recombination may lead to impairments not only in episodic, but also in semantic prospection. MTL contributions to scene construction and mental time travel may further compound impairments in amnesia on tasks that pose additional demands on these processes, but are unlikely to form the core deficit underlying amnesics' cross-domain future thinking impairment. Future studies exploring the role of episodic memory in other forms of self-projection or future-oriented behaviour may elucidate further the adaptive role of memory.

Studies of patients with amnesia have contributed greatly to our understanding of the neural and cognitive bases of episodic memory – our ability to retain and retrieve experiences from the past (Milner, Corkin, & Teuber, 1968; Squire, 1992). In the past five years, however, a growing number of investigators have become interested in episodic memory not only for its role in remembering the past, but also for its role in imagining or simulating possible future events. Evidence for the notion that memory and prospection are intimately linked comes from a number of different lines of research. Most prominent among those are (1) cognitive studies demonstrating that experimental manipulations, such as valence and temporal distance (D'Argembeau & Van der Linden, 2004; Szpunar & McDermott, 2008), as well as individual

* Mieke Verfaellie, PhD, and Elizabeth Race, Memory Disorders Research Center, VA Boston Healthcare System and Boston University School of Medicine, Boston, MA, USA; Margaret M. Keane, Department of Psychology, Wellesley College, Wellesley, MA, USA and Memory Disorders Research Center, VA Boston Healthcare System and Boston University School of Medicine, Boston, MA, USA
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Correspondence concerning this article should be addressed to Mieke Verfaellie, Memory Disorders Research Center (151A), VA Boston Healthcare System, 150 S Huntington Avenue, Boston MA 02130. E-mail: verf@bu.edu

differences (D'Argembeau & Van der Linden, 2006; Spreng & Levine, 2006), affect the phenomenological characteristics of autobiographical (episodic) memory and future event representations in the same way; and (2) neuroimaging studies in normal cognition, showing substantial overlap in the brain structures that are activated when subjects retrieve a memory from their autobiographical past or envision a future scenario (for review, see Schacter & Addis, 2009). Yet, the seeds for this thesis can be found in earlier case studies of patients with amnesia. In this paper, we review how these patient studies set the stage for current work on the cognitive and neural basis of future thinking. We then provide a brief review of recent neuroimaging studies, with an emphasis on the role of the medial temporal lobes (MTL) in future thinking, followed by a discussion of the specific MTL-mediated cognitive processes that may contribute to future thought. We then turn to more recent neuropsychological studies of prospection, with the goal of highlighting how these studies provide fertile ground for investigation of the link between episodic memory and future thinking and the role of the MTL in future thinking. We limit our review to studies of patients with amnesia. For a review of future thinking studies of healthy aging and dementia, see Addis and Schacter (2012).

Amnesia: The atemporal personal present

The hallmark of amnesia is the inability to remember autobiographical experiences from the past. Although less emphasised, early descriptions of patients with amnesia also comment on patients' inability to conceive of their own future. In his seminal treatise on Korsakoff's syndrome, Talland (1965) noted patients' inability to formulate personal plans and the fact that questions about the personal future were answered only with generalities. Tulving (1985) provided similar evidence in patient KC, a patient with profound amnesia secondary to a head injury (for further evidence see Rosenbaum, Gilboa, Levine, Winocur, & Moscovitch, 2009). KC's difficulty envisioning personal events in the future parallels his inability to recall a single event from his personal past: when asked what he would be doing tomorrow, KC answered that he did not know, and described his state of mind as blank. Based on these observations, Tulving hypothesised a close relationship between episodic memory and episodic future thought.

Tulving suggested that episodic memory is characterised by autonoetic consciousness, the ability to experience one's existence in subjective time extending from the personal past to the present to the personal future. A key process linked to autonoetic consciousness is the ability to mentally travel in time (Suddendorf & Corballis, 2007; Tulving, 1983; Tulving, 2002). Tulving argued that episodic memory is critical to the ability to detach from the

present, and project oneself into the past or the future. The parallel deficits in past and future in KC, then, were thought to reflect his impairment in autonoetic consciousness, the awareness typically associated with episodic memory.

A more systematic investigation of memory and future thinking was reported in patient DB, who developed amnesia following cardiac arrest (Klein, Loftus, & Kihlstrom, 2002). DB was given a 10-item questionnaire asking him to recollect personal events from the past (e.g., do you remember the last time you went to see a doctor?) as well as a 10-item questionnaire asking him to imagine personal events in the future (e.g., when will be the next time you go to a restaurant?). Past and future probes were matched for temporal distance. Accuracy of future events was scored based on their perceived plausibility. DB was highly impaired in generating both past and future episodes.

In parallel to the assessment of his "lived" (episodic) past and future, DB was also probed about his "known" (semantic) past and future. He was given 7-item questionnaires asking him to describe issues and events in a variety of public domains, one focusing on issues that had taken place during the past 10 years (e.g., what were some of the most important political events?), and the other focusing on issues likely to take place over the next 10 years (e.g., what will be some of the most important issues facing your community?). DB provided 4 out 7 correct answers to past questions, and 6 out of 7 to future questions – a performance that was judged to be relatively intact. Importantly, it appeared that his answers to future questions were not simply reinstatements of past issues, but rather, demonstrated that he was able to anticipate changes in the future. Taken together, these findings were interpreted as evidence that the dissociation in amnesia between impaired memory for the episodic past and preserved memory for the semantic past may also extend to the ability to anticipate the future. Returning to Tulving's conceptual framework, DB illustrates impaired autonoetic consciousness, but preserved "noetic" consciousness associated with semantic memory. Noetic consciousness allows one to think about future scenarios without mentally pre-experiencing a specific event.

While these case reports are informative in establishing a link between episodic memory and episodic future thinking, they do not allow inferences about the neural basis of the future thinking impairment, because of patients' extensive brain damage (in the case of Korsakoff patients and KC) or limited information about the site of damage (in the case of DB). We therefore turn next to neuroimaging studies in normal cognition.

A core network for memory and prospection

The first neuroimaging study to evaluate the neural basis of future thinking was a PET study in which participants were asked to talk freely about either the near or distant past or the near or distant future (Okuda, Fujii, Ohtake, Tsukiura, Tanji, Suzuki et al., 2003). Compared with a control condition involving semantic processing of words, significant activation was observed in prefrontal and medial temporal regions, both in the past and future conditions. Further, several regions, including the left parahippocampal gyrus, were more active during thinking about the future than about the past. Although providing initial evidence for the overlap between neural systems involved in memory and prospection, inferences from this study are somewhat limited because participants were not probed about specific events, and thus, it is unclear whether they provided specific memories and future simulations, or more general semantic information about the past and future.

Subsequent studies have taken advantage of the temporal resolution of fMRI and have probed participants about specific events. Addis and colleagues (Addis & Schacter, 2008; Addis, Wong, & Schacter, 2007) asked participants to first construct a past or future event in response to a cue, and then to further elaborate on the constructed event. There was common past and future-related activity in the left hippocampus and in posterior visual regions in the construction phase. In the elaboration phase, there was even more extensive overlap in the neural regions engaged by the past and future task, encompassing regions of the MTL, prefrontal cortex, posterior cingulate, and retrosplenial cortex. Other studies using somewhat different experimental conditions (Botzung, Denkova, & Manning, 2008; Szpunar, Watson, & McDermott, 2007) likewise revealed that medial prefrontal cortex, MTL, and midline parietal regions are similarly engaged when participants think about personal past and future episodes.

Taken together, these studies provide evidence for the notion that there is a core network of regions that supports both remembering the past and envisioning the future (Buckner & Carroll, 2007; Schacter, Addis, & Buckner, 2008). Moreover, many of the regions within this system are selectively correlated with one another in a large-scale network that includes the hippocampus. This network, commonly referred to as the default network, is active not only during autobiographical memory and future thinking, but also during other forms of simulation, such as navigation and theory of mind tasks (Buckner & Carroll, 2007; Spreng, Mar, & Kim, 2008).

The role of the MTL in prospection: Neuroimaging studies

The overlap in neural regions involved in memory and future thinking, and specifically posterior cortical regions (i.e., cingulate cortex, parahippocampal cortex, and hippocampus), has focused attention on the potential cognitive processes that may be shared between these disparate activities. In particular, the neural findings have been taken as evidence that as people think about the future, contents of memory are accessed. Several lines of evidence provide support for this view. As described above, Addis et al. (2007) observed that the neural overlap between past and future thinking was most pronounced in posterior regions during elaboration of the event, presumably as participants were drawing on the contents of memory to expand on their future simulations. Addis and Schacter (2008) further demonstrated that left posterior hippocampal activity was directly correlated with the amount of detail retrieved in both past and future events. Finally, in another study activity in the left hippocampus was more pronounced during past and future thinking in the personal compared to nonpersonal, conceptual domain (Abraham, Schubotz, & von Cramon, 2008). Given the greater demand on autobiographical memory retrieval in the former condition, these findings provide further support for the notion that the MTL is important for the retrieval of episodic elements from which future event simulations are constructed.

Additional clues to the processes involved in future thinking come from comparisons across conditions that are associated with differential activity in the MTL. Specifically, several studies have demonstrated that the MTL (Okuda et al., 2003; Weiler, Suchan, & Daum, 2010b), and in particular the anterior right hippocampus (Addis, Cheng, Roberts, & Schacter, 2011; Addis, Pan, Vu, Laiser, & Schacter, 2009; Addis et al., 2007) is more active when imagining than when remembering events. Schacter and colleagues have proposed that imagining future events requires the flexible recombination of details retrieved from memory into a coherent simulation. Such recombination of details is thought to depend on relational processing mediated by the hippocampus (Schacter & Addis, 2009). Further support for this view comes from the finding of greater MTL activity for temporally distant compared to temporally close (Addis & Schacter, 2008; Weiler et al., 2010b), and for low-probability compared to high-probability future events (Weiler, Suchan, & Daum, 2010a), on the assumption that binding event features into temporally distant or unlikely events poses greater relational demands.

In a related vein, Hassabis, Kumaran, and Maguire (2007) have suggested that the hippocampus and surrounding regions (parahippocampus, retrosplenial cortex) are critical for retrieving and integrating details from memory into a coherent scene. In one study, subjects recalled previously constructed fictitious scenes, imagined novel fictitious scenes, or remembered recent epi-

sodic events. All three tasks engaged the hippocampus, parahippocampal gyrus, and other core regions of the default network. Based on these findings (as well as patient data discussed below), the authors proposed that these regions mediate the construction, maintenance, and visualisation of complex spatial layouts – processes shared between real memories and imagined events. These spatial layouts are thought to form the scaffolding that enables additional event details to be integrated into a coherent whole.

The studies by Hassabis, Kumaran, and Maguire (2007) and Hassabis and Maguire (2007) are noteworthy in that they did not explicitly ask participants to imagine events in the future. Thus, their findings suggest that activation in the MTL and other core network regions is not tied to projecting oneself into the future. Further evidence that future projection is not a key process comes from the finding that imagining events in the past and in the future engages similar core network regions, including the hippocampus (Addis et al., 2009). Conversely, evidence suggests that tasks that draw equally on the future but differ in the specificity of events that are envisioned differ in their hippocampal dependence (Addis et al., 2011).

Returning to the specific role of the MTL in future thinking, two studies have highlighted the possible role of the parahippocampal gyrus. In the first study (Szpunar et al., 2007), participants were asked to remember past events, to envision future events, or to imagine specific events involving a familiar person (Bill Clinton). The latter condition was included as a control condition that involved many of the same processes as the former two, but lacked a sense of representing oneself in the future. There was marked overlap in activation associated with remembering the past and envisioning the future in a number of posterior regions, including posteromedial parietal cortex, parahippocampal cortex, and superior occipital gyrus. These regions were much less involved during the control task. Szpunar et al. (2007) hypothesised that this pattern of activation reflected the role of these regions in the reinstatement of familiar visuospatial contexts. Consistent with this notion, the same pattern of activation was obtained in a follow up study when participants thought about personal events in a known context, but very little activation was obtained when participants thought about personal events in unfamiliar contexts (Szpunar, Chan, & McDermott, 2009). Thus, it was suggested that both remembering the past and envisioning the future involve reinstatement of familiar contexts from memory. These parahippocampally mediated contextual associations could then, through hippocampal mediation, be recombined into novel scenes (Hassabis & Maguire, 2007) or integrated with other episodic details (Schacter & Addis, 2009) to create coherent and/or elaborate future simulations.

In summary, despite differences in the specific role postulated for MTL regions, neuroimaging studies broadly agree that envisioning the future

depends on retrieval of information from the past. One of the limitations of imaging studies, however, is that they are correlational in nature, and thus, while they clearly show that MTL regions are *active* during future simulation, they cannot address whether these regions are *necessary* for task performance. We next discuss how recent patient studies have started to enrich understanding of the role of the MTL in future thinking.

The role of the MTL in prospection: Amnesia studies

Initial evidence that the hippocampus is indeed critical for event simulation comes from a study by Hassabis, Kumaran, Vann, and Maguire (2007), who asked five amnesic patients with documented hippocampal lesions to imagine novel experiences. Patients were told to construct new experiences, and not to retrieve ones from the past. Most of the probes did not specify a time frame, and thus the task did not inherently require projecting oneself into the future, although the possibility cannot be ruled out that patients spontaneously envisioned an event in the future. Four of the 5 patients showed significantly impaired performance, and their mental representations were experienced as being more fragmented and lacking in spatial coherence. For instance, in response to the prompt "imagine that you are lying on a white sandy beach in a beautiful tropical bay," a patient responded only being able to see the colour of the blue sky and the white sand. The fifth patient performed as well as controls. This patient had previously been described as having hippocampi that were small, but within normal limits (McKenna & Gerhard, 2002), and further neuroimaging evidence supports the notion that residual hippocampal function in that patient may have been sufficient for task performance (Mullally, Hassabis, & Maguire, 2012). Residual hippocampal function has also been offered as an explanation of preserved future thinking in patients with developmental amnesia (Cooper, Vargha-Khadem, Gadian, & Maguire, 2011; Hurley, Maguire, & Vargha-Khadem, 2011; Maguire, Vargha-Khadem, & Hassabis, 2010; but see Kwan, Carson, Addis, & Rosenbaum, 2010), although it is also possible that patients with early damage are able to develop compensatory strategies, mediated by extra-hippocampal regions, to support task performance (Cooper et al., 2011; Hurley et al., 2011).

Taken together, the findings from Hassabis, Kumaran, Vann et al. (2007) offer the first lesion evidence for a direct link between hippocampal functioning and event simulation. Further, given that patients' impairment was particularly marked with regard to the spatial coherence of generated scenes, the authors concluded that the fundamental deficit in amnesia is one of scene construction.

In direct contradiction to these findings, Squire, van der Horst, McDuff, Frascino, Hopkins, and Mauldin (2010) reported that 6 amnesic patients with

MTL damage (5 with damage limited to the hippocampus and 1 with more extensive MTL damage) performed as well as controls in constructing future scenarios in response to cue words. Their performance was indistinguishable from controls in terms of the number of details and the number of words in their narratives, as well as in terms of ratings of vividness, emotion, and personal significance. These findings were interpreted as suggesting that future thinking does not depend on processes mediated by the MTL, and instead, is supported by regions outside the MTL. However, two aspects of this study are of note. First, whereas Hassabis, Kumaran, Vann et al. (2007) constrained subjects' responses with specific cues, Squire et al. (2010) imposed virtually no constraints on responses, providing single word cues but accepting responses that were unrelated to those cues. The absence of any constraint on subject responses may have disproportionately advantaged amnesic over control subjects. Second, patients in that study were also asked to describe autobiographical memories from their recent and remote past, and while the patients with hippocampal-only damage were impaired in recall of recent autobiographical events, they performed normally in recall of remote autobiographical events. This finding contrasts with other studies of hippocampal amnesia, which have demonstrated a pervasive autobiographical memory deficit encompassing the remote past (Rosenbaum, Moscovitch, Foster, Schnyer, Gao, Kovacevic et al., 2010). As such, the study from Squire et al. (2010) does not provide a strong basis to probe the effect of autobiographical memory on future thought.

In our own work (Race, Keane, & Verfaellie, 2011), we asked 8 MTL amnesics to recall events from the near and distant past, and to construct events in the near and distant future. Narratives were scored using an adapted autobiographical interview scoring procedure (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). A representative sample of a future event narrative generated by an amnesic patient and control is provided in Figure 1. Patients provided fewer episodic details (including event, time, place, perceptual, emotion/thought details) in their descriptions of both past and future events than controls, but provided a similar number of semantic details (including both autobiographical and non-autobiographical semantic details). Distant events were characterised overall by fewer episodic details, but the extent of impairment in amnesia did not differ as a function of temporal distance. Moreover, although all but one of the patients in this study had extensive MTL damage that extended beyond the hippocampus, one patient with a lesion limited to the hippocampus performed very similarly to the other patients, suggesting a critical role for the hippocampus in future event simulation.

The tasks used to assess future thinking in amnesia depend on the construction of an extended narrative, and as such, require the online integration of information in working memory. Given the role of the MTL in binding

Cue: Imagine catching your grandchild getting into trouble twenty years from now.

Patient: Twenty years from now, I'll be in my seventies. I catch my grandchild drinking and I explain the trouble I got into as a teenager drinking, what drinking can lead to in the future, prolonged use of it, as well as the short-term effects, and hopefully get them on the right path. I would imagine I would be visiting and I would be thinking I wish I was that young again and stupid. It's kind of hard to imagine stuff.

Control: This grandchild has come to visit me and I'm living in a senior centre by that time with my own apartment. The child has come on her own, flown in. What the child is doing is doping. That's still an issue. I know it because I can smell it. I approach the child in the afternoon, it's been going on the night before after I went to bed and she's in a single room, it's not a big complex that I'm in. The next morning I have a conversation with her. I don't accuse, I just ask how long. I assume she knows that I know. I have a discussion in that way. I ask her what's going on in her schools. I'll ask if her family knows that she's using. When she goes out the next morning to pick up groceries I discover the butts and some ashes. So the conversation is a hard conversation. By that time she's in her twenties so we have a straightforward discussion about how this is affecting her life. I'll ask her not to do drugs in my house. I'm troubled and I'm angry a little bit because she lies at first. It's just going to be me and that child. For me the relationship for that child is much more important, I'm not wanting to get her into difficulty. I don't know in twenty years hence that it'll be a problem.

Figure 1

Representative sample of future event narratives generated by an amnesic patient (top) and a control subject (bottom) when instructed to imagine catching a grandchild getting into trouble twenty years from now

information in working memory (Hannula, Tranel, & Cohen, 2006; Olson, Page, Moore, Chatterjee, & Verfaellie, 2006), the question arises as to whether future-thinking impairments in amnesia may reflect impairments in MTL-mediated narrative construction, rather than in future thinking per se. To examine this possibility, we additionally gave patients detailed drawings of scenes and asked them to tell a story about what was happening in each scene. In this condition, details, including the visuo-spatial layout, did not need to be retrieved from memory, as they were visually provided, but patients again had to construct a narrative. Examples of a patient and control narrative are provided in Figure 2. Hippocampal damage did not disrupt performance in the picture description condition, suggesting that (1) the MTL is not necessary for the online construction and integration of narrative content (although it may be involved in other aspects of narrative discourse, see Kurczek & Duff, 2011); and (2) impairments in future thinking in MTL amnesia are not due to demands on narrative construction, but rather, to the same kinds of demands on detail generation, recombination and/or scene construction that characterise remembering the past. In further support of this view, we found that performance on the past recall and future thinking tasks was highly correlated, but performance on the picture description and future thinking tasks was not (Race et al., 2011).

Cue: Imagine the picture is a scene taken from a movie and tell a story about what's going on in the scene.

Patient: It's a movie about a family who are at the park, two children, a boy and a girl. The boy looks younger than the girl. The girl is coming down the slide. Also children a ways away, two, one running to a swing and another running away from it. The squirrels are having a field day. One is going up a tree with something in its mouth that it took from the basket. The other one is going into the basket. Dad or the man is sleeping, ignoring everything. The mother looks like she was eating, she has a can of something in her hand and she's reading a book and totally oblivious to the children. The little boy also has a teddy bear that he brought that's on the blanket. Looks like they were eating a chicken leg and muffin. Two cans of soda on the blanket and a baseball nearby.

Control: The movie could be a day at the park. You could see the mother sitting on the bench, reading a book. The father's under a tree. One squirrel climbing up the tree, another squirrel into the lunch basket. Two people, a young lady sliding down a slide and a little boy at the end of it. Beyond them is a swing. There are trees, a red blanket, food in the basket, couple cans of soda, plate. Lady reading the book has a plate on the bench. Everybody seems to be having a good time. The father's sleeping and the mother's reading, kids are sliding. And they live happily ever after.

Figure 2

Representative sample of picture narratives generated by an amnesic patient (top) and a control subject (bottom) when instructed to describe a story about what' s going in a scene

In light of the finding in neuroimaging studies that hippocampal activation is greater for future simulations that are temporally distant than near (Addis & Schacter, 2008; Weiler et al., 2010b), the finding in our study that temporal distance did not affect patient performance may seem surprising. However, there is evidence that activity in some extra-hippocampal MTL regions is correlated with the temporal proximity of future events (Addis & Schacter, 2008; Okuda et al., 2003). Possibly, therefore, these two effects may have cancelled each other out in patients with more extensive MTL lesions. In this regard, a recent case study of an amnesic patient whose lesion was limited to the hippocampus is of interest (Andelman, Hoofien, Goldberg, Aizenstein, & Neufeld, 2010). The patient was administered the future events questionnaire developed by Klein et al. (2002) on several occasions. In the chronic stage of her illness, she was able to adequately answer questions pertaining to later today or tomorrow, but not further into the future, consistent with the notion that the demands on the hippocampus are greater in generating temporally distant than near events.

Paralleling the neuroimaging literature, neuropsychological studies have focused overwhelmingly on patients' ability to envision *episodic* events in the future. This emphasis is understandable, in light of the report from Klein et al. (2002) that their patient DB was able to envision future issues pertaining to public domains, such as politics and scientific discoveries (see also Andel-

man et al., 2010). Recently, however, we have undertaken a more detailed examination of patients' future semantic simulation performance (Race, Keane, & Verfaellie, in preparation). Two factors motivated this study. First, as mentioned above, Abraham and colleagues (2008) compared brain activation during personal, episodic, future thinking and nonpersonal, semantic, future thinking. Although a number of dissociations were observed across tasks (including greater left hippocampal activation for episodic future thought), there was also considerable overlap between the two tasks, including common neural activity in the MTL. This finding suggests that semantic future thinking, like episodic future thinking, may depend on MTL-mediated processes. Second, prior case reports yielding intact performance in amnesia (Andelman et al., 2010; Klein et al., 2002) have queried semantic future thinking at a less detailed level of analysis than typical episodic future thinking tasks, leaving open the possibility that amnesic patients might be impaired when the task requires generation of more detailed semantic scenarios.

In our study (Race et al., in preparation), patients were first asked to generate general semantic facts about the past and future in response to probes, analogous to the procedure used by Klein et al. (2002) (e.g., imagine the presidential elections in 2032; describe the 3 most important foreign policy issues that will be discussed in the election). They were then asked to elaborate in detail on one of the issues they had mentioned, by discussing why it was important and how it would impact on people's lives. Amnesic patients listed as many issues as controls, regardless of whether the past or future was probed, consistent with earlier findings (Andelman et al., 2010; Klein et al., 2002). However, when probed to elaborate, they provided impoverished descriptions of both past and future that were lacking in detail. Their descriptions were characterised by a reduction of general semantic and temporal semantic details, as illustrated by sample elaborations of an amnesic patient and control participant in Figure 3. As in the episodic domain (Race et al., 2011), memory and future thinking in the semantic domain were highly correlated, both in patients and in controls.

These results yield two important insights. First, just as episodic memory and episodic future thought are closely linked, so are semantic memory and semantic future thought (Suddendorf & Corballis, 2007). This link is consistent with the idea that the content of memory is mined in generating content for future scenarios, regardless of the memory domain. Second, taken together with results from previous studies, it appears that the impairment in amnesia is determined not by the episodic vs. semantic nature of future thought, but rather, by the level of detail required by the task. D'Argembeau and Mathy (2011) have recently provided evidence that the construction of episodic future thoughts involves access to knowledge structures at different levels of specificity: general knowledge of one's personal future, including

Issue Cue: Imagine it is 20 years from now and a special government report is published about the most important job skills and professions of the day. What will be the three most important job skills or professions profiled in the report?

Patient: teacher, engineer, administrator

Control: computer programming, genetics, energy

Elaboration Cue: For one of these issues, describe why it will be important and how it will affect people's lives.

Patient: In the engineer category, tools. Designing tools to have them do a better job is going to be a real important thing. And it is creative in the sense that the setting keeps changing, the priorities of what we need people to do.

Control: Computers are going to increase in our lives. Computers play a large part in cars and TVs now, later we'll see smart houses and smart apartment buildings where computers turn on the lights and control things. Like someone's not home, power will go down. Law enforcement right now aren't up to speed in computers, but they're trying. In London they have cameras, but don't have them linked to a network to recognise a crime. That could be it. That would mean more in-city surveillance. As things get bigger, there'll be more networks that need to be organised. If they're not organised they may collapse from time to time. There are smart things that do more than you think, but if they get attacked, people will die.

Figure 3

Representative sample of future semantic issues generated by an amnesic patient (top) and a control subject (bottom) when instructed to list the three most important job skills or professions 20 years from now, and elaboration of one of the future issues

conceptual information about the self and generic event scripts, is accessed first; this general knowledge provides the context for subsequent retrieval and integration of episodic details. Analogously, in the semantic domain, general conceptual knowledge about the world may provide the framework for the retrieval and integration of semantic details. An important difference between the two domains, however, concerns the level of specificity that is inherently required. Given that episodic future thinking probes are intrinsically temporally and spatially specific, access to specific mnemonic details is mandatory. In the semantic domain, by contrast, the level of information accessed may be determined by the nature of the probe. The general probes we used to elicit future issues may focus retrieval at a higher level of semantic information that is available to amnesic patients, possibly through accessing representations in lateral temporal neocortex. The probes asking for elaboration, on the other hand, may target more detailed semantic information that is not available to amnesic patients.

There is now substantial evidence that episodic memory can support retrieval from semantic memory (reviewed in Greenberg & Verfaellie, 2010).

In a similar vein, episodic memory may be used in semantic prospection to cue semantic details, which then could form the building blocks of semantic future narratives. Amnesics' impairment in providing richly detailed semantic narratives could thus reflect the role of the hippocampus in indexing detailed memory traces. An alternative, but not mutually exclusive possibility, is that the hippocampus is needed to recombine and integrate these details into a coherent semantic narrative. A similar claim for binding impairments outside the episodic domain has recently been made by Rosenbaum and colleagues (2009). They found that patient KC had difficulty reconstructing semantic narratives, such as fables and fairy tales with which he was familiar prior to his injury, but performed as well as controls in discriminating true from false narrative details.

Although future studies will be needed to elucidate the core MTL mediated processes that underlie the amnesic future thinking impairment across episodic and semantic domains, a consideration of the characteristics of semantic future thinking may help narrow potential candidate processes. For instance, since semantic future thinking does not require autonoetic awareness, it is unlikely that the fundamental impairment in amnesia is one of mental time travel. Similarly, it seems unlikely that scene construction is at the root of the joint impairment, as envisioning future nonpersonal semantic issues does not obviously depend on the construction of spatial contexts. A more plausible candidate mechanism underlying the joint impairment in episodic and semantic future thinking is the deficit in detail generation and/or recombination discussed above. This is not to say that other processes, such as mental time travel and scene construction cannot additionally contribute to the impairment in episodic future thinking. Indeed, a role for these additional processes in episodic future thinking can be inferred from the fact that while patients were impaired in both semantic and episodic future thinking, the impairment was more pronounced in the episodic than in the semantic domain (Race, Keane, & Verfaellie, 2010).

Future thinking in context: The role of the MTL in other non-mnemonic activities

The close link between memory and future thinking illustrated in the research reviewed here provides evidence for the adaptive value of memory, in that the MTL memory system provides the building blocks for future thoughts and simulations, both in terms of representational elements and in terms of underlying processes. Yet, it is also clear that the adaptive function of memory is not restricted to constructing simulations pertaining to the future. As highlighted above, Hassabis, Kumaran, and Maguire (2007) and Hassabis, Kumaran, Vann et al. (2007) have offered evidence for the role of the MTL in imag-

ination more broadly, irrespective of the need for future projection. In light of such findings, and the substantial overlap in neural substrates engaged by a variety of tasks that require mental simulation, it has been argued that the MTL may be involved any time a mental perspective is created that is not elicited by the immediately present environment, whether it be simulating a different time, space, or mental perspective (Buckner & Carroll, 2007; Spreng & Levine, 2006).

Yet, such an account may be overly broad. Preliminary evidence suggests that not all forms of mental simulation depend on memory for the past. One example concerns theory of mind, the ability to take on another's mindset. Rosenbaum, Stuss, Levine, and Tulving (2007) tested two patients with severe autobiographical memory impairment on a variety of theory of mind tasks and found that patients performed as well as controls. Future studies will be needed to discern the conditions under which tasks that require mental simulation, including theory of mind, pose demands on episodic memory.

Just as mental simulation may subserve performance in a number of cognitive domains, so may simulation of future events. A paradigmatic example is planning for the future. Based on an analysis of the unfolding content of thought as participants constructed future events, D'Argembeau and Mathy (2011) found that representations of future events are often linked to personal goals. Specifically, they demonstrated that, when simulating a future event, participants initially access general knowledge structures, which are commonly organised around personal goals. This general knowledge then cues specific event representations that instantiate these goals. Although planning is a complex, multi-dimensional process, the ability to simulate specific events that enable realisation of these goals and to modify plans depending on the outcome of such simulations, is likely an important component of planning. Consistent with this view, Andelman et al. (2010) reported that their amnesic patient, who was impaired at event simulation, was also unable to plan for the future. Given the fact that this patient had normal executive function abilities, her planning impairment was likely linked to impaired simulation of the future. It is currently unknown whether the MTL is important for the formulation of goals or only for the construction of specific simulations that allow goal implementation. An important area for future work will be to further delineate the role of the MTL in planning and other forms of future-oriented behaviour (e.g., Sheldon, McAndrews, & Moscovitch, 2011).

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