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Episodic memory and event construction in aging and amnesia

Kristoffer Romero [a,*], Morris Moscovitch [a,b]

[a] Department of Psychology, University of Toronto, Canada
[b] The Rotman Research Institute, Baycrest, Toronto, Canada

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ABSTRACT

Construction of imaginative or fictitious events requires the flexible recombination of stored information into novel representations. How this process is accomplished is not understood fully. To address this problem, older adults (mean age = 74.2; Experiment 1) and younger patients with MTL lesions (mean age = 54.2; Experiment 2), both of whom have deficient LTM compared to their respective controls, were given a setting (e.g. jungle) and 3–6 words (e.g. tiger, tree, snake) and asked to imagine an event in that setting by relating the words to each other. Both older adults and patients showed deficits in forming coherent mental representations relative to younger adult and healthy control groups, respectively. Moreover, the ability to form coherent events was associated with subsequent memory for the items. These findings suggest that deficits in LTM, or processes mediating it, are one factor that affects event construction, which in turn leads to poorer encoding and/or retention of the studied materials. These results have implications for theories of the cognitive processes underlying the construction of imaginative events in the laboratory and everyday life.

Introduction

The functional utility of a memory system that can obligatorily store and retrieve unique events consciously must go beyond mere retrospection: as the Queen in *Alice's Adventures in Wonderland* noted, "It's a poor sort of memory that only works backwards" (Carroll, 1886, p. 56). Confirming the Queen's pronouncement, an emerging body of evidence suggests that LTM interacts with, and contributes to, various cognitive tasks, such as problem solving (Chen, Mo, & Honomichl, 2004; Sheldon, McAndrews, & Moscovitch, 2011) and imagination (Hassabis, Kumuran, & Maguire, 2007; Hassabis, Kumuran, Vann, & Maguire, 2007). Of particular interest is imagination, which involves construction of mental representations of novel events, whether deliberately (i.e. prospection) or inadvertently (i.e. daydreaming) (Delaney, Sahakyan, Kelley, & Zimmerman, 2010; Hassabis & Maguire, 2009; Pillemer, 2003). This ability to construct a novel mental representation has been posited as a means by which humans use memory to guide decision-making and subsequent behavior: specifically, generating possible future outcomes may allow us to pre-experience the consequences of choices before they happen, thus giving useful feedback provided such representations are accurate approximations of real-life (Atance & O'Neilll, 2001; Benoit, Gilbert, & Burgess, 2011; Boyer, 2008; Buckner & Carroll, 2007; Gilbert & Wilson, 2007; Peters & Büchel, 2010; Schacter & Addis, 2007).

The processes that govern imagination are beginning to be elucidated. It is clear that imagining a novel event depends, in part, on retrieving relevant information from episodic memories of similar experiences and their concomitant neural substrates. Evidence from studies of patients with brain lesions (Addis, Sacchetti, Ally, Budson, & Schacter, 2009; Hassabis, Kumuran, & Maguire, 2007; Hassabis, Kumuran, Vann, et al., 2007; Rosenbaum, Gilboa, Levine, Winocur, & Moscovitch, 2009), of functional

* Corresponding author. Address: Department of Psychology, University of Toronto, 100 St. George Street, Toronto, Ontario, Canada M5S 3G3. Fax: +416 978 4811.
E-mail address: kris.romero@utoronto.ca (K. Romero).

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neuroimaging of healthy people (Addis, Pan, Vu, Laiser, & Schacter, 2009; Addis & Schacter, 2008; Addis, Wong, & Schacter, 2007; Addis et al., 2009; Hassabis, Kumuran, & Maguire, 2007; Hassabis, Kumuran, Vann, et al., 2007; Okuda et al., 2003; Spreng, Mar, & Kim, 2009) and even of electrophysiological studies in rats (Johnson & Redish, 2007), have suggested that the hippocampus, a structure long-known to be necessary for formation and retrieval of episodic memories in long-term memory (LTM; Scoville & Milner, 1957), is also implicated during construction of imaginary or anticipated events. Other structures that form part of the autobiographical memory and default network, such as the medial parietal and medial prefrontal cortex, are also recruited (Buckner, Andrews-Hanna, & Schacter, 2008; Spreng et al., 2009). This evidence has led investigators to propose that one function of LTM, mediated by the hippocampus and related structures, is to supply elements from long-term episodic memory that are needed for event construction (Buckner & Carroll, 2007; Hassabis & Maguire, 2007, 2009; Moscovitch, 2008; Schacter & Addis, 2007).

In addition to retrieval, another key aspect to imagining a novel event is the actual construction of the mental representation itself (i.e. event construction). Because an imaginary event has not been previously experienced, it cannot be evoked in its entirety merely by retrieving items from memory. To imagine a novel, coherent event, these items must be recombined or reordered in new ways (Rosenbaum et al., 2009; Schacter & Addis, 2007; Suddendorf & Corballis, 2007), and it is presumably the coherence of a constructed event (or lack thereof) that would dictate whether imagined items in consciousness are perceived as a unified scene/event, or merely unrelated mental images (Addis & Schacter, 2012; Blumenfeld, Parks, Yonelinas, & Ranganath, 2010; Hassabis, Kumuran, & Maguire, 2007; Hassabis, Kumuran, Vann, et al., 2007; Hassabis & Maguire, 2009). Furthermore, given that one property of episodic memory is that information is encoded in a manner that it may be flexibly recombined, and that episodic memory retrieval is a reconstructive process, it is reasonable to expect that constructing/recombining information into a coherent mental representation is an important aspect of imagination (Bartlett, 1932; Eichenbaum & Cohen, 2001; Martin, Schacter, Corballis, & Addis, 2011; Morris, Bransford, & Franks, 1977; Roediger & McDermott, 1995; Schacter & Addis, 2007; Schacter, Norman, & Koutstaal, 1998).

The processes that govern event construction, however, are still poorly understood. To date, most imagination studies have used an open-ended cueing paradigm, emphasizing the creation of detailed imagined scenes/events: such a task would require both retrieving episodic and semantic elements from LTM in response to a general cue (e.g. imagine a beach scene), and then constructing the imagined event from those elements. Consequently, variations in task performance may be due to differences in the ability to search memory and retrieve the requisite elements from LTM (e.g. umbrella, beach balls, people playing volleyball, etc.), and/or from differences in recombining and binding of retrieved elements into a coherent representation. Some evidence suggests that imagination performance depends partially on event construction ability. Studies of patients with hippocampal lesions have shown that in addition to being sparsely detailed, the imagined scenes produced by patients are also rated as less-coherent by the patients themselves and by raters (Hassabis, Kumuran, & Maguire, 2007; Hassabis, Kumuran, Vann, et al., 2007; Rosenbaum et al., 2009; though see Maguire, Vargha-Khadem, & Hassabis, 2010; Squire et al., 2011). It is not clear, however, whether the patients' deficit in retrieving details from memory precluded them from constructing spatially coherent scenes, or whether two separate deficits exist.

Indeed, in a recent review, Addis and Schacter (2012) identify initial retrieval and elaboration as two of the many process involved in imagination, noting that less is known about the processes and neural substrates governing event constructions. Drawing on Hassabis et al.'s findings regarding the importance of coherence in scene construction, we reasoned that coherence may also be implicated in event construction. Evidence from humans with medial temporal lesions and fMRI in healthy controls suggests that the hippocampus is implicated in a variety of processes, such as transitive inference (Preston, Shrager, Dudukovic, & Gabrieli, 2004), maintaining continuity across discourse (Duff, Gupta, Hengst, Tranel, & Cohen, 2011; Duff Hengst, Tranel, & Cohen, 2009) and story-telling (Schmitter-Edgecombe & Creamer, 2010; Rosenbaum et al., 2009) all of which would suggest a role for the hippocampus in constructing coherent events.

Recent evidence has indicated that aging is also associated with deficits in successfully incorporating specific event details (i.e. 'person, place, and object') during imagination tasks (Addis, Musicaro, Pan, & Schacter, 2010). When given three details to incorporate into an imagined event, older adults showed a deficit in integrating all the details within one time period. However, it remains unclear whether this was due to poor construction of an event per se, or due to other age-related cognitive changes, such as decreased monitoring ability or manipulation within working memory (Osaka, Logie, & D'Esposito, 2007; Petrides, 2005).

A related question is whether there are consequences for how well an imaginary event is initially constructed: Specifically, how does the coherence of a constructed event relate to its subsequent memory? One might predict that more coherent imagined events would be remembered better than less coherent ones, perhaps because of more elaborative encoding and organization that boosts recall for those items (Bower, 1970; Craik & Lockhart, 1972; Staresina, Gray, & Davachi, 2009). This interpretation is supported by a recent finding that hippocampal activation for an imagined event predicts subsequent memory for it (Martin et al., 2011) but no-one has shown more directly that the coherence of the imagined event is a contributing factor.

Taking these concerns into account, we constructed a novel task similar to those of Summerfield, Hassabis, and Maguire (2010) and Addis et al. (2010) that separates retrieval of the elements of the event from the construction process itself. By testing older adults with episodic memory loss presumably caused by medial temporal lobe deterioration, and amnesic people with confirmed MTL lesions, we hoped to gain insight into the contribution of episodic memory and the MTL to event construction. If deficits in