



Episodic memory and event construction in aging and amnesia

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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.

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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'Neill, 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

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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 processes 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

event construction, and subsequent memory, in these populations are still evident when the elements comprising the event are provided, then the impairment cannot be ascribed simply to impaired retrieval of goal-relevant information, but must also include processes implicated in the construction and retention of these elements into a coherent narrative (Craig & Salthouse, 2000; Hasher, Zacks, & May, 1999; Mitchell, Johnson, Raye, & D'Esposito, 2000; Old & Naveh-Benjamin, 2008).

In Experiment 1, we compared younger and older adults' event construction and subsequent memory performance when the elements for constructing the event were provided rather than requiring the participants to retrieve the elements from LTM themselves (as in Summerfield et al., 2010). Participants were shown a "context" word such as "jungle" and 3–6 words such as "tiger, tree, snake" and were asked to imagine a novel event by relating the various objects that were named to one another within that imagined context. Providing names for the to-be-imagined events allowed participants to complete the task with minimal retrieval demands, so that performance would be based largely on event constructional ability, rather than differences in retrieving the required elements from LTM. In addition, by varying set size from three to six items, we hope to extend previous research on imagination by examining at what level of mnemonic load do event construction deficits appear, if such group differences exist.

Given the recent debate as to whether the MTL are truly necessary for constructing novel events (See Addis & Schacter, 2012 for a review), in Experiment 2, we tested patients with confirmed MTL lesions and amnesia, who were otherwise cognitively intact. Doing so allowed us to determine directly whether MTL damage impairs the ability to construct coherent imagined events. Moreover, we could ascertain whether the predicted deficits in event construction in older adults are due in part to MTL-mediated episodic memory functions, one aspect of cognitive functioning that declines with age.

Experiment 1

In this experiment, we examined whether aging is associated with changes in event construction ability, and whether the coherence of an imagined event mediates its subsequent memory. As we noted, younger and older adults were shown a "context" word and 3–6 "item" words on a computer screen, and were asked to construct an imaginary event by relating the presented item to one another in that the target context. With the words still visible on the screen, the event was then described out loud, and the responses were recorded, and later transcribed and scored. Providing items for the to-be-imagined events for the duration of the trial ensured that differences in event construction performance would be based largely on differences related to the construction process itself, by reducing the effect of LTM demands during the task since the participant did not have to hold them in memory during the construction phase. Group differences in performance were compared at different set sizes, to determine whether event construction varies as a function of age.

To determine whether event construction ability plays a role in subsequent memory for constructed events, we used a cued recall paradigm to probe memory of the stimulus items five min following the construction task. If the coherence of the imagined events enhances memory for the individual items, then creating more relations between items within an imagined event should be associated with recall of those items. Since coherence in scene construction is reduced in people with amnesia related to MTL damage (Hassabis, Kumaran, & Maguire, 2007; Hassabis, Kumaran, Vann, et al., 2007), we hypothesized that age-related memory decline would affect event construction coherence in a similar manner. This led us to predict that the events older adults construct would be less coherent, given the deterioration of the MTL with age, and as a result their memory for the constructed events would be worse than that of young adults.

Method

Participants

Twenty-four younger adults and 26 older adults participated in the study. All participants were native-English speakers and had no prior history of any major neurological or psychological illness. Group demographics are listed in Table 1. All older adults were living independently within the greater Toronto area, and were recruited through ads in the local newspaper. All younger adults were first-year psychology students at the University of Toronto. Testing took place over a single session, lasting approximately two hours. Participants gave informed consent prior to their participation in the study. For their participation, older adults were remunerated \$20, and younger adults were awarded course credit. This study was approved by the Research Ethics Board at the University of Toronto.

Stimuli

A total of 132 words were taken from the MRC psycholinguistics database (Coltheart, 1981), of which 24 were used for context descriptions (i.e. BEACH), and the remaining 108 words were used as items to be imagined within each context. All context lists were approximately equivalent in terms of word length (range = 4–8 letters, $M = 5.43$, $SD = 1.27$), frequency (range = 1–125 per million, $M = 30.08$, $SD = 28.12$), concreteness (range = 425–637, $M = 581.90$, $SD = 39.26$), imageability (range = 454–642, $M = 579.91$, $SD = 39.04$), and familiarity (range = 381–644, $M = 531.34$, $SD = 51.91$).

Item words were not counterbalanced or randomized for each context word, because doing so would have resulted in highly implausible combinations of items and contexts, despite the fact that all word stimuli were highly familiar. Instead, item words were yoked to context words such that every item word could plausibly occur within the given context, but would not be found exclusively within that context (i.e. a jacket in a basement, vs. a polar bear in the Arctic). Context and item word sets were presented randomly to avoid order effects. To test for potential word differences across set size conditions, several one-way ANOVAs were conducted using the mean frequency, imageability, and familiarity, and word length for each set size.

Table 1
Demographics and neuropsychological test scores for younger and older adults.

	Young adults	Older adults	<i>p</i> -Value
<i>n</i>	24	26	
Age	18.5 (1.35)	74.15 (6.47)	
# Right-handed	22	23	
Years of education	12.92 (.57)	15.28 (3.14)	
Word span	4.70 (.70)	4.35 (.63)	=.07
Alpha span	4.13 (.69)	3.69 (.68)	<.05
Letter-number sequencing (max = 21)	–	9.8 (2.08)	
Logical memory immediate recall (max = 75)	–	40.54 (10.93)	
Logical memory delay recall (max = 50)	–	25.54 (9.39)	

Standard deviations (*SD*) listed in parentheses.

There were no significant differences for any of the word attributes (frequency, $F(3,104) = 1.27$, $p = .29$; imageability, $F(3,104) < 1$; familiarity, $F(3,104) = 1.68$, $p = .18$; word length, $F(3,104) < 1$).

Procedure

Participants were tested individually in a quiet testing room. Following informed consent, participants were given the construction task. Approximately five minutes following completion of the construction task, participants completed cued recall of the item words used in the construction task, using the context words as a cue. In addition, all participants were given word span and alpha span, simple span measures of working memory (Craig, 1986) and older adults were given additional measures of WM (Letter-number sequencing) and LTM (Logical memory) from the Wechsler Memory Scales–3rd Edition (Wechsler, 1997). These additional measures were not given to the younger adults because of concerns regarding restricted variance of scores within this age group, which may limit the likelihood of detecting meaningful correlations. Both logical memory and letter-number sequencing were administered following cued recall of items from the construction task, to avoid interference effects from those items.

Construction task. The experimental session consisted of one block of 24 trials, with six trials per set size. On each trial, following a fixation cross, participants were shown a context word (i.e. STADIUM), which was paired with a varying number of item words (set size: 3, 4, 5, or 6 words). Participants were told to imagine the items together within the event or scene described by the context, and to describe that event out loud. Specifically, participants were told to imagine as many relations between the items as possible, and to be sure to explicitly state those relations out loud. For example, for items ‘APPLE, DESK, PENCIL, BOOK’ and the context ‘SCHOOL’, participants should say something like, “Inside a school room, there’s a desk with a book on it. On top of the book is an apple with a pencil sticking out of it.” Participants were told that it was not sufficient to just say the words out loud or just form a sentence with the items (viz. Inside the school there was a desk, a book, an apple and a pencil); they must try to imagine the event or scene, and how the items are related. Participants were given no time limit to describe their event or scene. All words were presented on the screen for the

duration of the trial. When the imagined event or scene was described in full, the participant pressed a key to end the trial. Following this, participants made self-report judgments on a 5-point Likert scale of the perceived difficulty of imagining the event or scene, and its subjective overall coherence.

Scoring. The imagined events and scenes were recorded via digital recorder and transcribed verbatim for scoring purposes. For each trial, the number of explicitly mentioned relations between item words was tallied, to give a measure of how related the constituent items were (i.e. *relational coherence*) as an index of event or scene construction ability. The rationale for this scoring was based on previous reports of associative deficits within older adults (Mitchell, Johnson, Raye, & D’Esposito, 2000; Old & Naveh-Benjamin, 2008), and by studies establishing the roles of the hippocampus in relational memory processes and imagination (Davachi & Wagner, 2002; Eichenbaum & Cohen, 2001; Hassabis, Kumuran, & Maguire, 2007; Hassabis, Kumuran, Vann, et al., 2007). We assumed that if participants produced a coherent imagined event or scene during the task, the relations between items should be available to verbal report. Moreover, highly coherent imagined events and scenes would have a larger number of relations between constituent elements, compared to those that are less coherent.

For example, for the items “BIRD, EDGE, MAILBOX, GRASS” and context ‘YARD’, the description “In my front yard, there was a bird at the edge of the grass. The bird was looking at the mailbox” would be scored as having four relations: yard-bird, bird-edge, edge-grass, bird-mailbox. In contrast, the description “There’s a yard outside, and inside the yard there’s a bird, and I also see a mailbox and some grass by the edge” would be scored as having two relations: yard-bird, grass-edge. The latter description would not be as coherent as the former, having fewer relations amongst the items. The description, “I see a yard, and some grass, and a mailbox, and an edge” would be scored as having no relations, because it is unclear how the items are present within the imagined scene. Moreover, in line with task instructions, only relations formed between stimulus words were counted in the scoring: relations between stimulus words and other items spontaneously included by the participant were not counted. This ensured that the measure of relational coherence is based only on event construction ability for the given stimuli, and is not

Table 2
Examples of relations for scoring of the construction task in Experiments 1 and 2.

Relation type	Description	Example	Related words
Spatial	Two items and their location to one another	"Then our boat got caught in some seaweed . We tried using a..." "I was climbing a tree in the park , when I saw a bunch of geese..."	BOAT-SEAWEED TREE-PARK
Temporal	Two items and their temporal proximity or sequence	"My boyfriend decided to read me a passage from his favorite poetry book, and then he proposed to me with a diamond ring..." "While they're staring at the moon , a frog jumps onto the girl's face..."	POETRY-DIAMOND MOON-FROG
Causal	Causal effect or inference between two items	"I handed the camera to my mother so that she could take a picture of the pony ..." "I won a prize for shooting an arrow through a balloon..."	CAMERA-PONY PRIZE-ARROW
Indirect	An explicit relation between two items via a third item	"The uniformed clerk took our luggage on the trolley ..." "The umbrellas were shading a small little boy playing with his ball ..."	UNIFORM-TROLLEY (via luggage) UMBRELLA-BALL (via boy)

influenced by whether or not participants differed in the amount of detail incidentally retrieved from memory during the task.

Examples of types of relations are listed in Table 2. For a relation to be counted between items, the participant must have explicitly stated the relation between them: assumed or inferred relations were not counted unless it was impossible to interpret the phrase any other way. Repetitions of relations between two item words were not counted. Also, any item word could have a described relation with multiple other item words, as long as they were stated explicitly. Scoring was done by the first author (K.R.), and a research assistant. Inter-rater reliability was tested by selecting 25 events at random and comparing scoring criteria: percent agreement between scorers was high (Chronbach's alpha = .95). Because of the contents of the transcribed narratives, it was not always possible to be blind to group membership. However, because the scoring criteria involved very little subjective judgment, scoring bias was not an issue.

In addition, we measured the word count of each trial response, to determine whether groups would differ in terms of verbosity. Finally, to determine whether or not subjects were prone to forgetting of recent responses during the imagination task, we tallied the number of item words per trial that were omitted across groups. Our rationale was that if older adults had somewhat poor memory for recent responses, they may also forget whether or not a given item word was already incorporated into their narrative, and thus fail to mention it altogether.

Results

Construction task

To determine whether age groups differed in terms of the relational coherence of their imagined events and scenes, we submitted the mean number of explicit relations in the construction task to an ANOVA with age (younger, older) as a between-subjects factor and set size (3, 4, 5, 6) as a within-subjects factor. This analysis revealed a main effect of set size, $F(3, 144) = 56.10$, $p < .001$, with more relations being formed as the number of items increased (Fig. 1). The main effect of age was also significant,

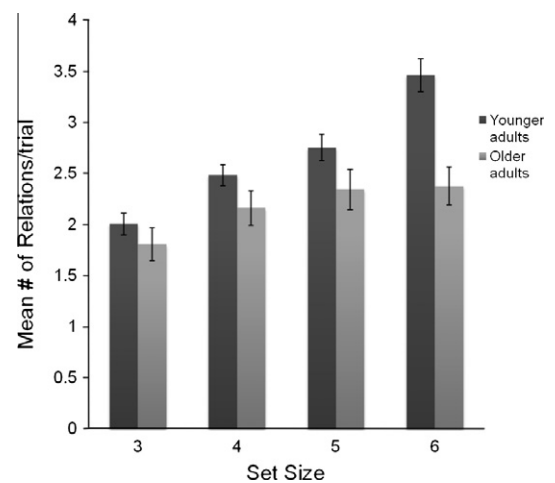


Fig. 1. Differences between older and younger adults in relations/trial (coherence score) at set sizes from 3–6 in Experiment 1.

$F(1, 48) = 9.14$, $p < .005$, with older adults producing fewer relations ($M = 51.92$, $SD = 17.35$) during their imagined events and scenes compared to younger adults ($M = 64.33$, $SD = 9.29$). The group by set size interaction was also significant, $F(3, 144) = 11.10$, $p < .001$. *T*-tests of simple effects showed that younger adults produced significantly more relations when constructing an event with five or six item words, $t(48) = 2.05$, $p = .05$ and $t(48) = 4.87$, $p < .05$, respectively. Other set sizes showed a trend toward group differences in performance (3 words: $t(48) = 1.13$, $p = .26$; 4 words: $t(48) = 1.91$, $p = .06$).

Verbosity

To test the possibility that performance on the construction task was confounded by verbal output, we calculated word counts for each participant's responses on each trial. Preliminary analysis suggested the distributions of word counts at all set sizes violated assumptions of normality (Kolmogorov–Smirnov $Z_s = 1.82$, 1.79, 1.51, and 1.73 for set sizes 3, 4, 5, and 6, respectively; all $ps < .05$). Thus, we log-transformed the word count data and submitted it to a mixed ANOVA with group and set size as the

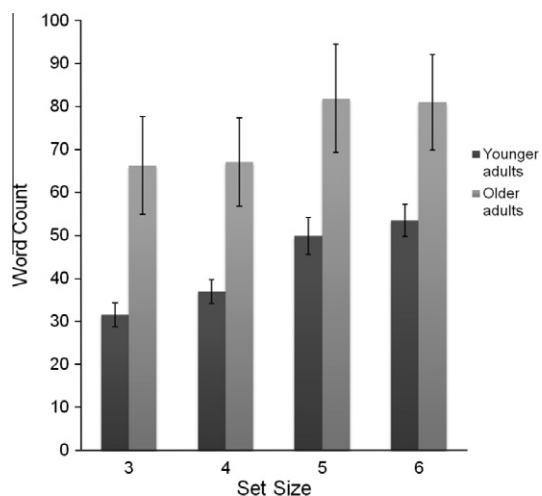


Fig. 2a. Differences between older and younger adults in the verbosity of responses during the construction task in Experiment 1.

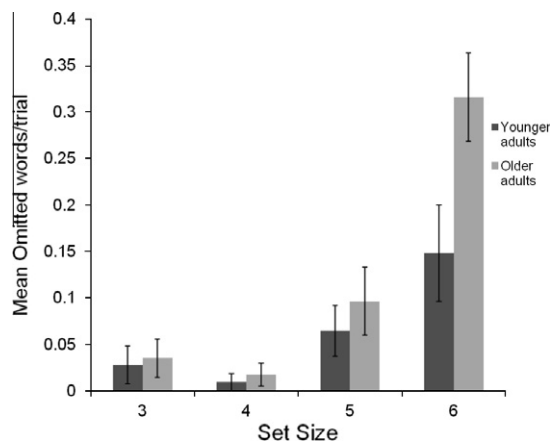


Fig. 2b. Differences between older and younger adults in omission rates at set sizes from 3–6 in Experiment 1.

between- and within-subjects variables, respectively. The main effects of set size and age were significant, with larger set sizes eliciting more lengthy verbal responses, and older adults producing more words than younger adults ($F(3, 144) = 131.07, p < .001$ and $F(1, 48) = 12.82, p < .005$, respectively). The group by set size interaction was also significant, $F(3, 144) = 11.38, p < .001$. Inspection of Fig. 2a clearly indicates that older adults were more verbose compared to younger adults, the difference varying as a function of set size. To investigate the contribution of verbosity to task performance, the average word count/trial was also computed for each participant, log transformed, and used as a covariate in the earlier ANOVA on relational coherence scores. Both the main effects of group and set size remained significant after accounting for individual levels of verbosity, $F(1, 47) = 12.78, p = .001$ and $F(3, 139) = 8.48, p < .001$, respectively. The group by set size interaction also remained significant, $F(3, 139) = 5.40, p = .002$. Thus, the age differences in task performance

could not be explained by differences in verbosity between groups.

Omissions

The rate of word omissions was very low in both groups at lower set sizes, resulting in non-normal distributions. Thus, group differences were compared at each set size using nonparametric statistics. Data from one older adult was an outlier and was excluded from the analysis. Mann–Whitney U -tests indicated that older adults were more likely to omit item words from their imagined scenes only at a set size of 6 ($U = 288, p = .69, U = 262.5, p = .15, U = 270, p = .45$, and $U = 177.5, p < .05$ for set size 3, 4, 5, and 6, respectively). This occurred despite the fact that the item words were present on the screen for the duration of the trial (Fig. 2b).

Self ratings of coherence and difficulty

Ratings of coherence and difficulty were entered into a mixed ANOVA with age and set size as between and within-subjects variables, respectively. There was a main effect of set size, $F(3, 144) = 4.69, p < .05$: with increasing set size, imagined events and scenes were rated as slightly less coherent, $M = 3.39, 3.21, 3.21$, and 3.15 for set sizes 3, 4, 5, and 6, respectively. The main effect of age was not significant, $F < 1$. The age by set size interaction was significant, $F(3, 144) = 2.67, p = .05$. With increasing set size, younger adults tended to report lower levels of coherence (Young: $M = 3.38, 3.14, 3.13$, and 2.95 for set sizes 3, 4, 5, and 6, respectively), compared to older adults (Older: $M = 3.40, 3.28, 3.30$, and 3.35 for set sizes 3, 4, 5, and 6, respectively). However, t -tests of simple effects at all set sizes failed to reach statistical significance ($t < 1$ for set sizes 3, 4, and 5; $t(48) = 1.45, p = .15$ for set size 6).

For difficulty, there was a main effect of age, with younger adults rating the task as more difficult (Young: $M = 2.42, 2.54, 2.85$, and 3.09 for set sizes 3, 4, 5, and 6, respectively), compared to older adults (Older: $M = 1.67, 1.89, 2.05$, and 2.10 for set sizes 3, 4, 5, and 6, respectively; $F(1, 48) = 12.06, p = .001$). The main effect of set size was also significant ($F(3, 144) = 21.08, p < .001$), with trials at higher set sizes being rated as more difficult, $M = 2.05, 2.21, 2.45$, and 2.60 for set sizes 3, 4, 5, and 6, respectively). The interaction was not significant, ($F(3, 144) = 1.84, p = .15$).

Cued recall

The number of words recalled from the construction task after a 5 min delay was entered into an ANOVA, again with age as a between-subjects variable, and set size as a within-subjects variable. There were significant main effects of set size and age, $F(3, 144) = 77.53, p < .001$ and $F(1, 48) = 31.97, p < .001$, respectively (Fig. 3). Not surprisingly, more words were recalled on trials with a larger set size, and older adults recalled fewer words ($M = 56.38, SD = 21.94$) compared to younger adults ($M = 83.38, SD = 10.30$). The interaction was also significant, $F(3, 144) = 9.72, p < .001$. Tests of simple effects revealed that younger adults recalled more words compared to older adults for all set sizes, with this difference increasing at higher set sizes (3 words: $t(48) = 3.39$,

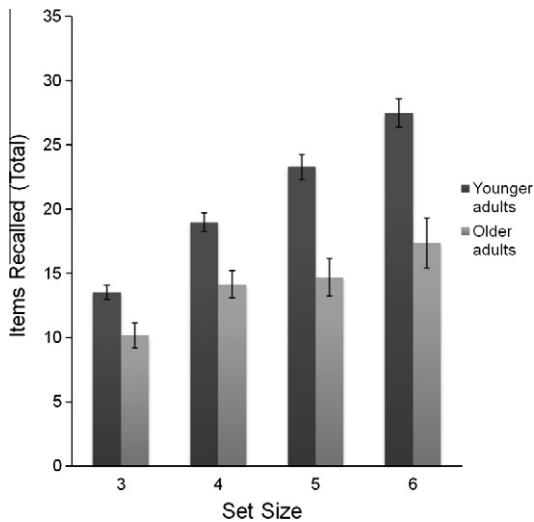


Fig. 3. Differences between older and younger adults in cued recall of task stimuli in Experiment 1.

$p = .008$; 4 words: $t(48) = 4.19$, $p < .001$; 5 words: $t(48) = 5.47$, $p < .001$; 6 words: $t(48) = 5.10$, $p < .001$).

Recall performance was also calculated as the proportion of words correctly recalled for each set size. Across conditions, younger adults recalled roughly 80% of item words, whereas older adults recalled roughly 60% at best (i.e. 3 words condition, $M = .56$), showing a non-significant decline in performance with more words (6 words condition, $M = .48$) (Fig. 4a). To determine if words that were successfully bound during the task were more likely to be subsequently recalled, we re-analyzed cued recall performance by calculating the proportion of recalled words that were part of an inter-item relation that was used during the event construction task. The main effect of group was significant, with younger adults showing a higher proportion of recalled words as part of an inter-item

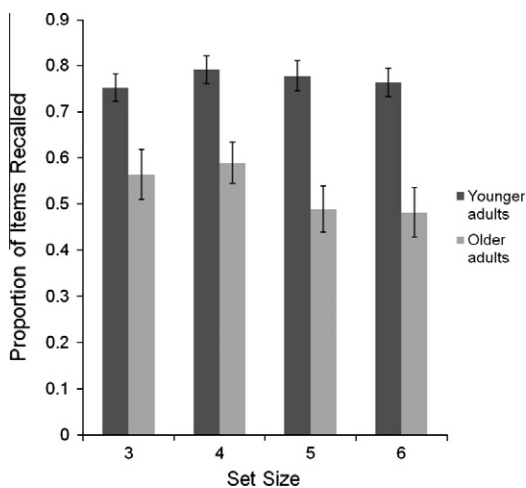


Fig. 4a. Proportion of stimuli recalled as a function of set size in younger and older adults in Experiment 1.

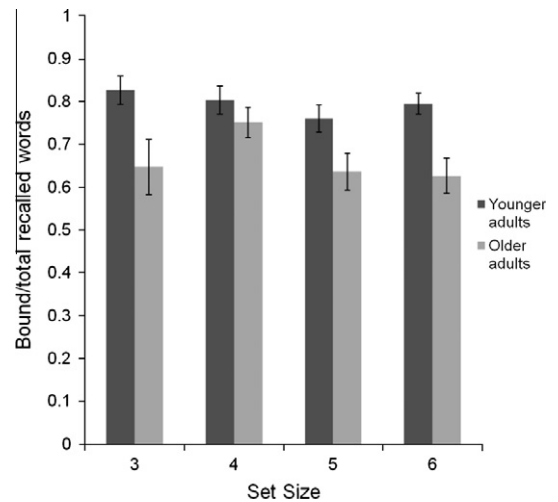


Fig. 4b. Proportion of bound versus total recalled words as a function of set size in younger and older adults in Experiment 1.

relation, compared to older adults, $F(1,48) = 12.65$, $p < .005$. The main effect of set size was also significant, $F(3, 144) = 3.21$, $p < .05$. The interaction was not significant, $F(3, 144) = 1.48$, $p = .22$ (Fig. 4b).

We also computed overall task performance and recall performance for each individual to examine individual differences in task performance and recall. Across age groups, forming more relations during the construction task was associated with higher recall scores (younger adults $r = .47$, $p < .05$; older adults, $r = .52$, $p < .05$), suggesting that creating more inter-item relations during the task improved subsequent memory for the items. In addition, within older adults, the total number of relations formed across trials (i.e. total coherence) was positively correlated with long term memory test scores (i.e. logical memory; $r = .41$, $p < .05$), but not with the two working memory measures (i.e. alpha span and letter–number sequencing; $r = .15$ and $r = .05$, respectively).

Discussion

In this experiment, we investigated whether older adults would show deficits in constructing novel events/scenes when the required information is provided and while varying mnemonic demands. Using this paradigm, one may have predicted that older adults would show deficits in performance compared to younger adults, due to age-related changes in cognitive functioning (Addis et al., 2010; Craik & Salthouse, 2000; Hasher et al., 1999; Mitchell, Johnson, Raye, & D'Esposito, 2000; Old & Naveh-Benjamin, 2008). However, it is possible that older adults' performance may have been superior to that of young adults because of other factors that improve with age, such as older adults' proficiency in telling coherent stories (Pratt, Boyes, Robins, & Manchester, 1989), intact ability to construct and comprehend a narrative (Radvansky & Copeland, 2001), and their well-developed semantic memory (Craik & Salthouse, 2000). Consistent with the former prediction, we found that older adults created fewer

relations between items in their imaginary constructions compared to younger adults, reaching significant differences at higher set sizes (i.e. set sizes 5 and 6). With larger sample sizes and more statistical power, it is likely that group differences would have reached significance at the lower set sizes as well. These results could not be explained by differences in overall words used or task difficulty, as older adults were more verbose and rated the task as less difficult, compared to younger adults. Finally, for older adults, the relational coherence was correlated with performance on standard tests of LTM, but not of working memory.

The age-related deficits in relational coherence parallel other studies showing relational processing deficits in older adults, due to declining hippocampal function (Mitchell, Johnson, Raye, & D'Esposito, 2000; Old & Naveh-Benjamin, 2008). For example, Ryan, Moses, and Villate (2009) reported age-related deficits in forming propositional relations on a transitive inference task. Older adults showed poorer performance in terms of acquiring the propositional relations, which was also correlated with neuropsychological measures sensitive to hippocampal function. Similarly, in our study, performance on a neuropsychological test of LTM in older adults was also positively correlated with relational coherence ability (see also Addis, Wong, & Schacter, 2008; Hassabis, Kumaran, & Maguire, 2007; Hassabis, Kumaran, Vann, et al., 2007).

Also, the coherence of a constructed event affected subsequent memory for the items, as relational coherence scores were correlated positively with cued recall of test items across both age groups. Importantly, items that were relationally bound were more likely to be recalled, and older adults recalled a lower proportion of bound items, suggesting that decreased ability to create associations between item words influenced their recall. It is well-established that the depth with which information is processed affects its subsequent memory, and that mental imagery and semantic elaboration are two types of deep processing (Bower, 1970; Craik & Lockhart, 1972). Thus, it is reasonable to infer that imagining items within a novel event/scene combines these forms of deep processing, and thus influences subsequent memory. Indeed, recent neuroimaging evidence suggests that the quality of an imagined event, which implicates the right anterior hippocampus, influences subsequent memory of an imagined event via the interaction between anterior and posterior regions of the right hippocampus (Martin et al., 2011).

Notably, the observed deficits in relational coherence cannot fully account for the age-related deficit in subsequent memory. Specifically, we observed that although subsequent memory for the constructed event was related to relational coherence in both older and younger adults, the proportion of bound items that were recalled was lower in older than in younger adults, indicating that poor retention was an added problem for the older group. This is supported by the finding that older adults showed an increased propensity to omit item words at the highest set size, suggesting that they had difficulty monitoring whether or not items had already been mentioned. One possibility is that these omissions were also due to deficits in retention: that is, at high mnemonic loads, older adults

had deficits retaining all the information over time. Results compatible with this interpretation were obtained recently by Gallo, Korthauer, McDonough, Teshale, and Johnson (2011) who tested younger and older adults on a future imagining paradigm, and measured memory for both the details of each event and source memory (i.e. task condition), one day later. Not surprisingly, older adults showed poorer memory for both source information and specific event details. Notably, however, older adults still showed poorer source memory for those events that they could recall in detail, suggesting that they had difficulty retaining information over time, be it specific event details, source information, or both.

Despite these clear patterns of age-related deficits in performance, subjective ratings of coherence and task difficulty did not parallel these objective measures of task performance. The fact that older adults rated the present task as less difficult despite showing poorer performance, suggests that their subjective perceptions of the task may be influenced by other factors. In this case, we suggest two possibilities. The first is that older adult's increased familiarity with such tasks was responsible for their lower ratings of difficulty. Anecdotally, many older adults reported that the task reminded them of reading to their children, and that they found the task easy to understand. Moreover, older adults would have more experience engaging in prospection, as humans may use this strategy in decision-making and problem solving (Boyer, 2008; Buckner & Carroll, 2007; Suddendorf & Corballis, 2007), particularly in their 30's and 40's, when major life goals require frequent future planning (i.e. relationships, family, work productivity; Conway & Holmes, 2004). A second possibility is that older adults' poor metamemory abilities (Dunlosky & Connor, 1997; Shah & Craik, 1989) lead them to underestimate task demands and prevents them from exerting the necessary effort needed to perform well (see also Hertzog & Dunlosky, 2011). Gallo et al. (2011) also found that subjective ratings of task performance were not related to source memory in older adults who completed a future imagining task, providing further evidence that such ratings in older adults may reflect other processes.

Although the findings from Experiment 1 fit well with other studies of age-related deficits in event construction and retention, other interpretations are possible. One is that age-related deficits in executive control or working memory, as opposed to some relational deficit, are driving the effects (Cabeza, 2002; Raz, 2000; Velanova, Lustig, Jacoby, & Buckner, 2007). That is, deficits in the ability to organize and combine information during the construction task were the source of poor performance (Simons & Spinners, 2003). Performance, however, was always self-paced with no response deadline demands, and items were always presented within a plausible context that provided a general schema for organization, thereby minimizing strategic organizational demands that typically implicate the prefrontal cortex (Blumenfeld & Ranganath, 2007). Indeed, older adults show reduced deficits in memory performance when relevant contextual information is provided (Castel, 2007; Hess, 2005). Performance also did not correlate with a measure of working memory, a test of frontal

function, though correlations may have been found with tests of frontal function that were not investigated in this study. Despite this, it is important to note that we do not mean to suggest that executive control processes do not contribute to event construction performance in older adults, but merely that they did not seem to be a limiting factor in the event construction task and performance measures we used. Under different conditions, it is possible that older adults' performance also would reflect the operation of executive components associated with WM.

Another possibility is that age-related deficits were due to older adults retrieving less conceptually-rich representations when given the cue words. That is, when shown an item word such as 'portrait', younger adults may bring to mind more conceptual associations, compared to older adults. However, aging is typically associated with slight increases in crystallized knowledge, suggesting that older adults have more conceptual information at their disposal (Craik & Salthouse, 2000). Thus, it is not likely that age-related change in the conceptual richness of mental representations can fully account for the present findings.

The results favor the interpretation that age differences in processes implicated in LTM were one source of the older adults' deficit on the event/scene construction task. To obtain stronger evidence that LTM is one factor that contributes to event construction, in Experiment 2 we tested people with MTL lesions who have severely impaired LTM but relatively preserved functions in other cognitive domains, including WM. If our hypothesis is correct, the deficits observed in older adults should be manifested to an equal or greater degree in patients, even though the material necessary for construction is readily available to them on the screen throughout the task. In addition, given the theoretical role of the MTL in creating coherent mental representations (Addis & Schacter, 2012), testing patients with MTL damage using our paradigm allows us to determine whether indeed event construction is dependent on MTL structures.

Experiment 2

Previous studies showing future imagining deficits in patients have used open-ended cueing paradigms, which do not allow for distinguishing whether poor performance is due to deficits in retrieving the elements that form the core of the constructed event, or due to some deficit in forming a coherent mental representation using those elements (Addis et al., 2009; Hassabis, Kumuran, & Maguire, 2007; Hassabis, Kumuran, Vann, et al., 2007; Squire et al., 2011). Race, Keane, and Verfaellie (2011) tested patients with hippocampal lesions on a future imagining task, and included a narrative construction control task, in which subjects had to describe a complex picture in great detail. They found that patients had less-detailed future scenarios but showed no deficits in producing a narrative of the picture compared to controls, suggesting narrative construction was not a factor in patients' future imagining performance. Although their task would appear similar to ours, there are a few key differences. In our task, patients had to construct a new event, rather than describe an

existing one, and although the items are always present on the screen, the relational, internal representations they form during construction of the event/scene must be held online in WM and/or encoded into LTM, as the task proceeds. By also varying the number of elements that need to be included in the event/scene we could determine whether the deficit in amnesic patients is exacerbated by the ensuing complexity of the construction.

If MTL-mediated LTM processes are indeed implicated in event construction, we would expect that patients would show larger deficits in event construction compared to controls. In addition, because of their large deficits in LTM, we would expect that they may be prone to deficits in monitoring their performance, as they would have difficulty encoding their imagined events, and thus would not recall earlier portions of their description (Squire et al., 2011). If this is the case, then patients should show increased omission rates at lower set sizes, compared to older adults, as well as much poorer memory for the stimuli, even if tested immediately following the task.

Methods

Participants

Six patients (one female) with damage to the MTL from the greater Toronto area participated in this study. All were native-English speakers and had isolated impairments in long-term memory, with no deficits in visual perception, language, executive functioning, attention, or simple measures of working memory. Group demographics and neuropsychological test performance are listed in Table 3. In terms of etiology, two patients suffered damage to the MTL due to epileptic seizures, and one of these patients had surgical resection of the right MTL. Two patients sustained damage due to viral encephalitis, one patient suffered from suspected Whipple's encephalopathy, and the final patient suffered anoxic damage due to an MCA infarction. To confirm damage was localized to the MTL, T1- and T2-weighted structural MRIs were obtained. Five out of the 6 patients received scans, with one patient dying before structural scans could be obtained (See Appendix A for representative structural slices).

Twelve controls (six females) that were matched as closely as possible to patients for age and education were recruited from the greater Toronto area. None of the controls had a history of major neurological or psychological illnesses.

Materials and procedures

The testing procedure was similar to that of Experiment 1. For patients, the testing session lasted 1 h, consisting of the construction task, followed by cued recall of the objects. In addition, information on performance on some neuropsychological tests was obtained prior to the experiment from clinical files. For the control participants, testing also took place over a single session, lasting approximately 2 h, with the construction task occurring in the first hour, and neuropsychological testing following subsequently. All participants gave informed consent prior to their participation, and were remunerated for their participation. This study was approved both by the Research

Table 3
Demographics and neuropsychological performance for groups in Experiment 2.

Patients	Age	Yrs Edu	DS Fwd (/14)	DS Bwd (/14)	DS Tot (/28)	LM 1 (/75)	LM 2 (/50)	FAS	Animals
1001	56	12	11	6	17	17	0	29	16
1003	37	12	11	8	19	28	8	29	19
1004	60	16	9	9	18	27	0	61	23
1005	58	16	9	6	15	38	18	47	25
1006	58	12	7	6	13	20	12	26	18
1007	56	16	–	–	12	–	–	–	–
Control (Mean)	50.85	15.67	11	7.17	16.4	47	29.5	49.55	23.73
t-Test (p value)	.47	.16	.11	.60	.71	<.01	<.01	.19	.12

Note: Yrs Edu = years of education; DS Fwd = Digit span forward; DS Bwd = Digit span backward; DS Tot = Digit Span total; LM 1 = Logical memory immediate recall; LM 2 = Logical memory delayed recall; FAS = Phonemic fluency; Animals = Semantic fluency.

Ethics Board at the University of Toronto and the Research Ethics Board at Baycrest Centre for Geriatric Care.

Scoring

We used the same scoring methods as in Experiment 1. For each trial, the number of explicitly mentioned relations between item words was tallied, to give a measure of how related the constituent items were (i.e. *relational coherence*) as an index of event construction ability.

In addition, we measured the word count of each trial response, to determine whether groups would differ in terms of verbosity. Finally, to determine whether or not patients were prone to forgetting of recent responses during the imagination task, we tallied the number of item words per trial that were omitted, similar to Experiment 1.

Results

Neuropsychological tests

Neuropsychological testing of the groups confirmed LTM deficits in all patients (Table 3). Notably, there were no other significant cognitive deficits between groups, suggesting that any group differences in task performance are due to memory-related factors, and not to other functions.

Construction task

The mean number of explicit inter-item relations formed during the construction task was entered into a mixed ANOVA with group (patient, control) and set size (3,4,5,6) as the between- and within-subjects factors, respectively. This analysis revealed a main effect of group, with patients producing fewer relations on average compared to controls, $F(1, 16) = 6.84, p < .05$, and a main effect of set size, indicating more relations were formed on trials with larger set sizes, $F(3, 48) = 24.79, p < .001$. The group by set size interaction was significant, $F(3, 48) = 2.86, p < .05$ (Fig. 5). Tests of simple effects showed that patients produced significantly fewer relations on trials of set size 3, 5, and 6, with a similar trend at a set size of 4 ($t(14) = 2.44, p < .05, t(14) = 1.90, p = .08, t(14) = 3.73, p < .01$, and $t(14) = 3.13, p < .01$ for set sizes 3, 4, 5, and 6, respectively).

Verbosity

To examine whether the observed effects were due to differences in verbal output across groups, we calculated word counts for each trial, and submitted the average word

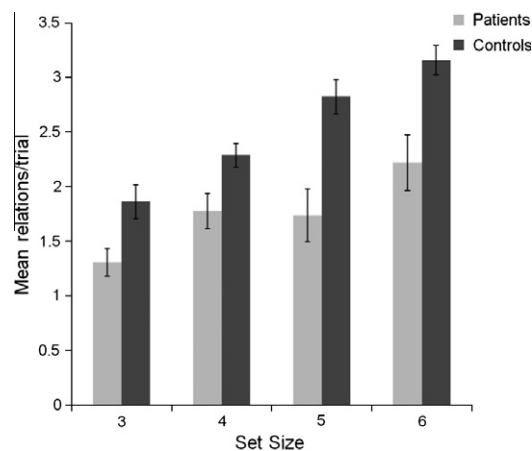


Fig. 5. Differences between patients and controls in relations/trial (coherence score) at set sizes from 3–6 in Experiment 2.

count per condition into an ANOVA using the same between- and within-subject factors. There was a significant effect of set size, with longer responses being produced at higher set sizes, $F(3, 48) = 24.68, p < .001$. Neither the main effect of group nor the group by set size interaction was significant ($F_s < 1.02$). Thus, verbal output per se could not account for patients' deficits in task performance.

Omissions

The mean number of item words that were shown on screen but omitted from the imagined scenes was submitted to a similar mixed ANOVA. The main effects of group and set size were significant, $F(1, 16) = 16.30, p < .01$ and $F(3, 48) = 9.43, p < .001$, respectively. In addition, the group by set size interaction was also significant, $F(3, 48) = 4.92, p < .01$ (Fig. 6). Tests of simple effects showed that patients omitted more words compared to controls at set sizes 4 and 5 (3 words: $t(16) < 1, 4$ words: $t(16) = 3.97, p < .005, 5$ words: $t(16) = 4.44, p < .005, 6$ words: $t(16) = 1.25, p = .23$). Generally, patients were more likely to omit item words from their imagined scenes, compared to controls. This occurred despite the fact that the item words were present on the screen for the duration of the trial.

Cued recall

Cued recall performance could not be collected for one patient, who had to leave the testing session early. Not

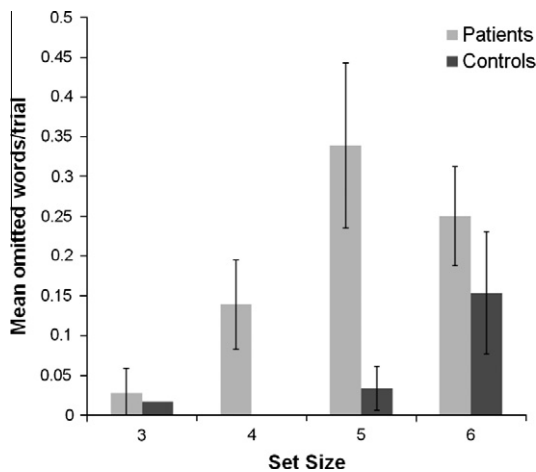


Fig. 6. Differences between patients and controls in omission rates at set sizes from 3–6 in Experiment 2.

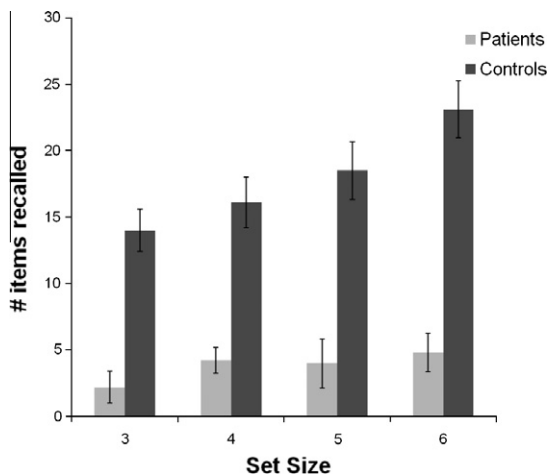


Fig. 7. Differences between patients and controls in cued recall of task stimuli in Experiment 2.

surprisingly, the main effect of group was significant, with patients recalling fewer items compared to controls, $F(1,15) = 25.21$, $p < .001$. In addition, the main effect of set size was significant $F(3,45) = 18.73$, $p < .001$. The group by set size interaction was not significant, $F(3,45) = 2.01$, $p = .15$ (Fig. 7). Inspection of Fig. 7 indicates that patients' performance at the cued recall task was close to floor for all set sizes. Consequently, analysis of the proportion of recalled words that were successfully bound was not calculated.

Subjective ratings

Ratings of coherence and difficulty were analyzed across groups in a mixed ANOVA. For coherence, the main effect of set size was not significant, $F(3,45) = 1.11$, $p = .35$, and the main effect of group was also not significant, $F(1,16) = 1.11$, $p = .31$. However, the group by set size interaction was significant, $F(3,48) = 2.82$, $p < .05$. Tests of simple effects revealed that there was a trend for controls

rating their events/scenes as more coherent at a set size of 3 only ($t(16) = 2.11$, $p = .051$). None of the other set sizes approached significance ($t(16) = .25$, $.24$, and 1.70 for set sizes 4, 5, and 6, respectively).

In terms of subjective difficulty, neither the main effect of set size, $F(3,48) < 1$, nor the main effect of group, $F(1,16) = 2.48$, $p = .14$, were significant. Similarly, the group by set size interaction was not significant, $F(3,48) = 1.53$, $p = .22$, suggesting that although patients performed more poorly compared to controls, they did not perceive the task to be more difficult.

Discussion

In this experiment, we sought to obtain more direct evidence that LTM processes, mediated by the MTL, are implicated in event/scene construction. Consistent with our prediction, patients with MTL lesions, and deficits restricted to LTM, formed fewer inter-item relations than did controls. These findings are consistent with the notion that patients with hippocampal lesions have difficulty creating spatially coherent scenes (Hassabis, Kumuran, & Maguire, 2007; Hassabis, Kumuran, Vann, et al., 2007), and formulating coherent narratives overall (Rosenbaum et al., 2009). Moreover, these results could not be due to differences in verbosity, as there were no group differences in terms of the length of descriptions. Thus, these findings confirm that LTM memory processes (i.e. encoding, retention, retrieval) dependent on the MTL are implicated during the construction of a novel mental representation.

Not surprisingly, patients performed at floor for subsequent memory of items immediately following the task, reflecting their impairment in declarative memory (Scoville & Milner, 1957). More interestingly, we found a propensity for patients to omit items, even at lower set sizes (i.e. 4), suggesting they had difficulty constructing an event/scene beyond a certain mnemonic load. We posit that patients were able to initially construct an event/scene, but had some difficulty encoding and retaining this information in LTM. Consequently, this information was not reliably available to be referenced as they continued their descriptions, resulting in fewer inter-item relations, and deficits in monitoring whether or not item words had been mentioned.

In contrast to task performance, patients did not show a consistent difference from controls in terms of their subjective ratings of coherence and difficulty. Damage to the MTL does not typically impair insight into general cognitive function or metamemory judgments, although accurate judgment on specific aspects of cognition may be more variable (Parkin, Bell, & Leng, 1988; Seelye, Schmitter-Edgecombe, & Flores, 2010; Shimamura & Squire, 1986). Given the nature of the present task, it is possible that because the items were provided and patients were generally able to complete the task, they may have adopted a different criterion in judging their performance, compared to controls. Previous studies of future imagining (Hassabis, Kumuran, & Maguire, 2007; Hassabis, Kumuran, Vann, et al., 2007) where patients report poorer ratings of performance used an open-ended cueing paradigm, which has significant LTM retrieval demands. This element of

retrieval would presumably influence patients' perceived task performance, perhaps accounting for the discrepancies between previous findings and our own.

General discussion

The purpose of these two experiments was to characterize processes involved in event construction, and to determine whether the quality of imagined events affects their subsequent memory. Experiment 1 provided evidence that older adults show deficits in event construction performance at higher set sizes that require more items to be integrated into a novel event. Also, we found evidence that the relative coherence of an imagined event/scene relates to recall of the items in both groups, and to older adults' LTM ability. We interpret older adults' constructive deficits relative to younger adults as reflecting age-related changes in associative processing. Furthermore, we found that aging is also associated with deficits in retaining imagined items in LTM, as evidenced by lower rates of recalling bound items among older adults, and by their increased omission rates. Experiment 2 provided more direct evidence that LTM processes that are mediated by the MTL contribute to the construction of novel events, as patients showed deficits on the construction task, both in terms of relational coherence and in terms of omission rates. Moreover, these deficits appeared at lower set sizes in patients, compared to older adults, indicating that more severe deficits in LTM affect the ability to construct a mental representation at a lower mnemonic load.

If the MTLs are critical for event construction, one might have expected the patient group to perform even more poorly compared to older adults. Although patients showed deficits at lower set sizes compared to older adults, they were still able to create some inter-item relations during the task. It may be that some inter-item relations generated by patients could be supported primarily by semantic memory, and these relations would still be counted in the scoring, resulting in patients being able to complete the task, albeit at a lower level of performance. Nevertheless, these associations represent only a small percentage (i.e. approximately 10%) of the responses produced by subjects as the ability to create further inter-item relations requires the flexible recombination of information, which is hippocampally-dependent. Moreover, although patients with MTL lesions can show deficits in semantic tasks under some conditions (Greenberg, Keane, Ryan, & Verfaellie, 2009; Sheldon & Moscovitch, 2012), these effects are minor in comparison to the patients' deficits in LTM (see Table 3). Thus, we think it highly unlikely that deficits in semantic memory account for the differences between patients and controls.

A novel finding was that across two experiments, older adults and patients both showed deficits in retention. Although relational coherence was correlated with subsequent memory in Experiment 1, older adults showed a lower likelihood of recalling relationally-bound items, compared to younger adults. Older adults also showed deficits in monitoring whether an item word was mentioned at higher set sizes. Addis et al. (2010) reported age-related deficits in combining specific details when imagining a

new event (i.e. 'person', 'place', 'object'). In this study, older adults had to recombine 1–3 previously provided items into an event, and showed deficits only at 3 items. These findings dovetail nicely with our own, and suggest that indeed, when an imagined event becomes sufficiently complex, some items are less likely to be integrated. Our results suggest that one reason for this is that with increases in set size, items are prone to omission due to poor retention of items in LTM.

Similarly, patients with MTL lesions showed a higher omission rate even when given four items. Squire et al. (2011) found that patients with hippocampal lesions were prone to repetitions when imagining the future, which would also be consistent with deficits in retention: if previously mentioned information cannot be reliably retained, it may either be mentioned again or not mentioned at all. Taken together, these findings suggest that successfully imagining a novel event requires the on-line retention of the mental representation during the construction process.

The results from Experiment 2 support the notion that brain structures implicated in forming and retaining associative information are involved in constructing novel mental representations, even when the elements that form the core of the constructed event are made available to the participant and remain present throughout the task. More generally, our results overall are in accord with cognitive neuroscience theories of imagination that posit MTL involvement in retrieval and/or reconstruction (Hassabis & Maguire, 2007, 2009; Schacter & Addis, 2007), and extend such theories by providing an initial characterization of event construction processes. Recent neuroimaging evidence suggests that when event construction occurs one item at a time, the hippocampus displays a biphasic pattern of activity, which may reflect ongoing retrieval and encoding aspects occurring in tandem (Summerfield et al., 2010). Other implicated structures include the entorhinal cortex, and parahippocampal gyrus (Diana, Yonelinas, & Ranganath, 2010; Davachi & Wagner, 2002), as well as prefrontal areas including the dorsolateral prefrontal cortex (Blumenfeld et al., 2010).

Although these experiments help characterize the event construction process, some questions remain. One question is the extent to which age and individual differences in how people approach a task influence imagination tasks in general. For example, research on narrative focus suggests that older adults may focus more on communication, rather than accurate description of the story (Harwood, Giles, & Ryan, 1995), and older adults are more prone to producing off-topic speech due to deficits in inhibiting irrelevant information (Hasher et al., 1999). Recently, Gaesser, Sacchetti, Addis, and Schacter (2011) have shown that older adults describe complex pictures qualitatively differently from younger adults (see also James, Burke, Austin, & Hulme, 1998; Mackenzie, Brady, Norrie, & Poedjianto, 2007). How precisely these effects and other age-related cognitive changes (i.e. declines in working memory) influence imagination performance warrants further investigation, using samples large enough to enable detection of more subtle contributions of these variables. Notably, there is some evidence that age-related declines in cognition may account for these shifts in narrative discourse,

suggesting that cognitive changes (normal or pathological) may underlie changes in both event construction and shifts in narrative style (Chapman et al., 2002; Fleming & Harris, 2009; Juncos-Rabadán, Pereiro, & Rodríguez, 2005).

It should also be noted that in this task, the to-be-imagined items were presented to participants: however, in a more naturalistic scenario such items would originate from LTM, from both the rich autobiographical experiences of the past, and the extensive network of semantic knowledge that the human brain can retain. In addition, although the task was designed to minimize retrieval demands from LTM, it is impossible to completely such demands from such tasks. The nature of the scoring criteria was such that only relations between provided items was counted, thereby limiting the influence of the amount of information retrieved from LTM on the present results.

Taken as a whole, these findings suggest that one aspect of event construction that changes with age and MTL dysfunction is the re-encoding of retrieved details into a novel event. The fact that the ability to form associations can impact the resultant imagined events may have implications for how we use (or misuse) memory in everyday life (Gilbert & Wilson, 2007; Schacter, 2004). Future research will need to identify and characterize situations in which event construction is implicated. For example, it is likely that certain types of prospective thoughts, subjective judgments, and predictions require event construction. Indeed, there is evidence of situations wherein hippocampal-mediated LTM does contribute to various social-personality aspects, such as defining the boundary conditions of one's personality (Klein, Cosmides, Tooby, & Chance, 2002), prospective delay discounting (Benoit et al., 2011; Peters & Büchel, 2010), predicting how one will feel in certain pleasant or unpleasant situations (Morewedge, Gilbert, & Wilson, 2005) and solving ill-defined problems (Schacter, Guerin, St. Jacques, 2011; Sheldon et al., 2011). More broadly, the results provide evidence that the utility of memory indeed extends beyond looking back, and that the human memory system is utilized in several adaptive fashions in daily life (Addis & Schacter, 2012).

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A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jml.2012.05.002>.

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