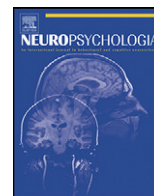




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Amnesia as an impairment of detail generation and binding: Evidence from personal, fictional, and semantic narratives in K.C.

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ABSTRACT

Autobiographical episodic recall involves active simultaneous generation and binding of various elements that were present during the initial experience. Deficits in this reconstructive process may account for some aspects of retrograde amnesia (RA) for personally experienced events. Constructive and reconstructive processes may involve similar mechanisms. If so, patients with extensive anterograde amnesia (AA) and RA should show deficits in non-recollective cognitive domains, such as imagining events that had never been experienced and recounting non-personal narratives, that presumably rely on constructive and re-constructive processes, respectively. To test these possibilities, patient K.C., who has severe AA and RA for personal episodes, was asked to generate fictional events and to recall and recognize details of well-known fairy tales and bible stories. K.C.'s performance on both tasks was better than expected given his severely impaired autobiographical episodic memory (AM), but significantly worse than that of control participants. K.C. was able to create a skeletal outline for both types of narratives, providing sufficient information to convey their gist, but the narratives were fragmented and lacking in detail. This deficit cannot be explained as resulting entirely from deficient stored semantic knowledge, because K.C. was able to discriminate between true and false details of non-personal semantic narratives on a recognition test, which he cannot do for personal events [Gilboa, A., Winocur, G., Rosenbaum, R.S., Poreh, A., Gao, F., Black, S.E., Westmacott, R., & Moscovitch, M. (2006a). Hippocampal contributions to recollection in retrograde and anterograde amnesia. *Hippocampus*, 16, 966–980]. Thus, retrograde AM impairment may be viewed as both a loss of information as well as a deficit in reconstructive processes that hamper or prevent the binding of information to generate a cohesive, detail-rich memory.

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Endel Tulving's reputation as an authority in memory research and theory was well-established before he met K.C., a person with severe anterograde amnesia (AA) and extensive retrograde amnesia (RA) for autobiographical episodes. Although Endel's ideas influenced empirical and theoretical advances in the cognitive neuroscience of memory, until he met K.C. his own work never left the confines of behavioral, experimental psychology. Almost from the beginning, Endel, K.C., and K.C.'s family developed a fruitful scientific partnership. It is not overstating the truth to say that Endel's collaboration with K.C. was at the centre of many of the major advances in human memory research in the last quarter century (for

a detailed review, see Rosenbaum et al., 2005). The current paper expands on findings presented at the Cognitive Neuroscience Society Meeting (Rosenbaum, McKinnon, Levine, & Moscovitch, 2003), as described in our 2005 review of studies with K.C., the topic of which has caught people's attention since the publication of a more extensive series of amnesic cases by Hassabis, Kumaran, Vann, and Maguire (2007). In honour of Endel's 80th birthday celebration, we thought it fitting to present these findings, as they address issues on reconstructive processes in autobiographical memory (AM) that are at the forefront of new developments in memory research and theory.

Early observations that K.C. was no more able to imagine details of future personal events than of past ones (Rosenbaum et al., 2005; Tulving, 1985, 2002; Tulving, Schacter, McLachlan, & Moscovitch, 1988) suggested that a common substrate may underlie AM and future imagining. These findings led to more systematic examination of the ability to generate events that never occurred in one's

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past in the absence of AM in another amnesic person, D.B. Klein, Loftus, and Kihlstrom (2002) first documented that D.B. had similar difficulties to K.C. in reconstructing past personal events and constructing future ones in response to a structured questionnaire. They demonstrated that this deficit did not extend to constructing possible public events, though the questions posed did not appear to promote the generation of detailed narrative responses. More recently, using brief descriptions of commonplace scenes as cues, Hassabis, Kumaran, and Vann, et al. (2007) reported an impaired ability to imagine new experiences in a group of amnesic persons with AM impairment. The imagined events were short on detail and lacked spatial coherence.

There are a number of interpretations of these data, ranging from deficits in auto-noetic consciousness/self-projection and scene construction to binding of details and loss of details from storage. Endel himself proposed that amnesia for episodic events is related to impaired auto-noetic (self-knowing) consciousness, a type of awareness that allows for the subjective re-experiencing of past personal events, as well as of imagining possible future events in which one might participate (Tulving, 1985).

Several related proposals have built on this idea. Buckner and Carroll focused on “self-projection” as the crucial common component in AM, future cognition, and related abilities, including imagining others’ thoughts and feelings (theory of mind, ToM) and certain aspects of navigation (Buckner & Carroll, 2007; but see Rosenbaum, Stuss, Levine, & Tulving, 2007; Rosenbaum et al., 2000). However, because the amnesic participants in Hassabis, Kumaran, and Vann, et al. (2007) showed impairment even when they were not explicitly required to imagine themselves in a scene, it was argued that deficits in self-projection are not the root of the disorder. Instead, these researchers proposed a third alternative that impairment of cognitive processes implicated in scene construction accounted for deficits in AM and future cognition.

Another view is that AM loss results from impaired relational processing that involves binding of co-occurring elements of an event (Davachi, 2006; Eichenbaum, 2004; Eichenbaum, Otto, & Cohen, 1994; Ryan, Althoff, Whitlow, & Cohen, 2000) that operate as much at acquisition as at retrieval, and may be necessary for constructing new imagined events (Schacter, Addis, & Buckner, 2007; Schacter et al., 2008). Such binding processes account for scene construction deficits and may also subserve non-spatial functions, such as future planning and problem solving. More generally, RA may reflect a deficit in reconstructing or reassembling details of the past, an ability that is needed to simulate future events, rather than a primary loss of details from storage (Schacter, 1999; Schacter et al., 2007, 2008). It is conceivable, however, that deficits in binding as well as loss of information underlie the full spectrum of deficits in RA. By this account, K.C.’s memory loss for personal incidents may be symptomatic of a general inability to generate details and/or bind them into a coherent representation. If so, he should find it equally difficult to construct detailed narratives of events that were never experienced, whether they resemble commonplace activities from childhood to more recent years, as to reconstruct detailed episodic and semantic narratives from long-term knowledge.

Here, we report two experiments in an attempt to narrow down these interpretations. In the first experiment, K.C.’s ability to construct stories of events that he never experienced was compared to ones that he had experienced, to determine if loss of episodic information contributes to his AM deficit. If such information is necessary for personal episodic memory, K.C.’s narratives should be impaired more for real than for imaginary scenarios relating to himself, because in the latter case, he is free to draw on other non-personal knowledge to create fictional events.

The second experiment was designed to determine if a deficit in binding could account for loss of reconstructive memory by eliminating the requirement for self-projection and by ensuring the

availability of all the details needed to construct the narrative. To do so, we tested K.C.’s ability to recall non-personal semantic narratives in the form of well-known fairy tales and bible stories. A recognition version was used to verify that K.C. had knowledge of all the elements within the narrative prior to engaging in a construction process. If self-projection is not needed and all elements are available, then any deficit exhibited by K.C. may be attributed to faulty reconstructive processes. A secondary goal in both experiments was to determine whether deficits in representing spatial details contribute to any deficiencies in performance by using a detailed scoring method that takes into account the richness of the narratives in terms of both the number and quality of details generated (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). Since the non-personal semantic narratives used in Experiment 2 contain little spatial content compared to interpersonal aspects (see also Dyer, Shatz, & Wellman, 2000; Mar & Oatley, 2008), any deficits observed on this test are unlikely to be due solely to deficits in scene construction.

1. Methods and Results

1.1. Participants

K.C. was 52 years old at the time of testing. He is right-handed with 15 years of formal education and suffered irreversible amnesia as a consequence of a traumatic brain injury from a motorcycle accident in 1981. Magnetic resonance imaging (MRI) performed in 1996 revealed a pattern of diffuse brain damage that includes almost complete loss of hippocampal tissue and clear signs of atrophy to the parahippocampus in both hemispheres (see Rosenbaum et al., 2005). Also of note is a large lesion in left occipital-temporal cortex, which extends into retrosplenial cortex, as well as lesions to medial occipital-temporal-parietal, medial occipital, and left frontal-parietal regions. Other limbic structures such as the mammillary bodies, the septal area, and the fornices are also noticeably atrophic. Neuropsychological examination conducted at the time of experimental testing are reported in Rosenbaum et al. (2005) and described only briefly here. Mental status on the Dementia Rating Scale was above the cutoff for dementia, with most points lost on the memory subscale. K.C. received a Verbal, Performance, and Full-Scale IQ of 99 on the Wechsler Abbreviated Scale of Intelligence. Language, visuospatial, and executive functions were likewise intact on a wide range of tests, other than phonemic fluency, which was in the borderline range. In contrast, K.C. was severely impaired on verbal and nonverbal tests of anterograde memory, including the Logical Memory subtest of the Wechsler Memory Scale-Revised (scaled scores of 4 and 0 on immediate and delayed recall, respectively), California Verbal Learning Test (acquisition: $T = 12$, short delay recall: $Z = -4$, long delay recall: $Z = -4$, and recognition discriminability: $Z = -3$), Rey Osterrieth Complex Figure (0/36 on delayed recall), and Warrington Recognition Memory Test (26/50 on words, 25/50 on faces). Finally, performance on standardized measures of autobiographical memory (Kopelman et al., 1990; Levine et al., 2002) verifies AA and RA for personal incidents and personal semantics.

Comparisons in performance were made with two groups of controls. The first group was tested on the fictional event test and included 4 men, closely matched in age ($M = 54$, $S.D. = 3.4$, range = 52–59) and education ($M = 15.3$, $S.D. = 1.5$, range = 14–17). The second group was tested on the semantic narrative test and included 6 men, matched in age ($M = 53.2$, $S.D. = 3.03$, range = 42–57) and education ($M = 15.6$, $S.D. = 1.14$, range = 14–17). All controls were right-handed and free from any neurological or psychiatric disorder and substance abuse. Informed written consent was obtained from each participant according to the ethical guidelines of the Baycrest Ethics Review Board in accordance with the Declaration of Helsinki.

1.2. Fictional event test

1.2.1. Procedure

K.C. and control participants were tested on a fictional event task designed to elicit in imagination events sampled from different life periods. The events were plausible in the context of the participants’ lives but they had never occurred. This test was designed to determine if K.C.’s AM deficit is specific to memory storage/retrieval or reflects a more general deficit in generation and binding together of details that is distinct from memory but, nevertheless, influences it. Using an interview structure and scoring procedure similar to the Autobiographical Interview (Levine et al., 2002), participants were asked to rely on their imagination and invent a detailed story about an event that they had never experienced but that was plausible from each of five specified life periods (childhood, adolescence, early adult life, middle adult life, and the past year). If unable to generate an event for any of the time periods in the free generation condition (akin to the ‘free recall’ condition in the Autobiographical Interview), a list of events that were known never to have been experienced (verified by a close family member or friend) were provided for each time period. Participants were instructed that a fictitious event must not last

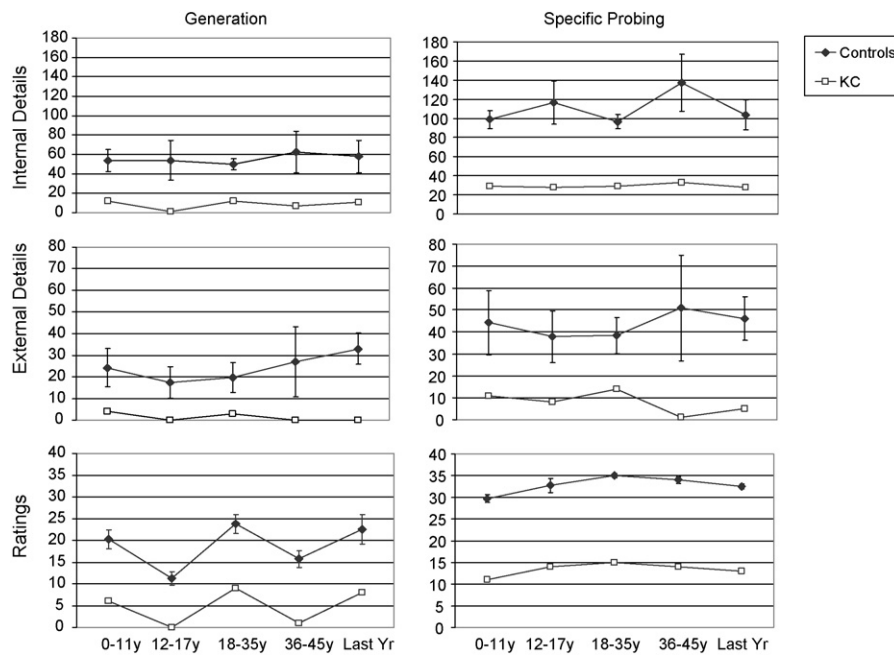


Fig. 1. Total number of details generated by K.C. and controls for internal (top row), external (middle row), and ratings (bottom row) categories across five imagined life periods when freely generated (left column) and when specific probes were made available (right column). Error bars indicate standard error of the mean for the control group.

for more than a few hours and were asked to imagine that they were personally experiencing the event at a specific time and place as they provided the description. The narratives were recorded verbatim and later transcribed for scoring purposes. Following the free generation condition, predetermined cues were used to gauge the limits of detail generation by providing additional structure. Task instructions remained in full view throughout the session, and reminders in the form of excerpts from K.C.'s own constructions were provided when needed to ensure that his anterograde memory deficit was not affecting his ability to remain on track while telling a fictional story. At the end of the interview, participants and their family members were questioned to further ensure that specific details of the constructed events did not resemble ones that had been experienced in the past.

Scoring was conducted by two independent raters who were highly trained on the Autobiographical Interview and blind to group assignment. Fictional details contained within the resulting narratives were first characterized as internal (episodic-like) or external (mostly semantic-like or schematic). Internal details were then categorized as central to the main event or as temporal, spatial, perceptual, or

emotional. External details were categorized as tangential/unrelated to the main event, semantic-like, repetitions, or metacognitive/editorializing. The number of details in each category was counted. Complementary qualitative ratings were also assigned to each of the internal detail categories, with the possibility of attaining a maximum of 3 points for each category except for detail richness, which was extended to 6 points to capture better the overall experiential nature of the narratives (i.e., overall maximum = 18 points). Quantitative and qualitative analyses were included in order to account for the possibility that two narratives that otherwise appear to be equally rich based on qualitative criteria may differ, nonetheless, on the number and type of details provided. Only a few minor discrepancies were noted between the raters, and these were resolved by discussion.

1.2.2. Results

K.C. was unable to generate a single detail unless supplied with a list of topics and a feasible introductory sentence. Similar to the results from the Autobiographical Interview (for comparison, see Rosenbaum, McKinnon, Levine, & Moscovitch,

KC: First Pet

I guess I'd go out with my dad and buy it, we'd go up to the pet store and get a dog, an Irish Setter, and it would be a puppy. We'd bring him home, and I don't know what he'd be called, I think I'd call him, I don't know what I'd call him. We'd have to put a stake in the backyard, I guess, to tie him up, get a collar and link it to the clothesline and tie him up.

Control 1: Getting Lost

The story starts when I was maybe 10 years old and I was in the countryside. Like, usually in the summer, my mother and the rest of the family went for these hot summer days, we tried to spend in the countryside. We rented, which was like a cottage or something, and uh, at that time, a lot of people, they were trying to collect blueberries in the forest, and I joined two somewhat more mature girls than I am, and I went with them to a forest, which was maybe 2 or 3 km away, and while we were there picking the blueberries, somehow I see something glittering further away. And, I was obviously curious about it and went much further. And, before I knew it, I separated from the other people and, eventually, realized I got lost, but I managed to reach a river, and I thought that if I keep going along the river, I would find some people. And, probably, it took me about an hour or two before I found somebody, and I asked him, I told him that I got lost and whether he could help me. Well, fortunately, that person was from the same, around the same place, and I managed to get back. Meanwhile, my companions were panicking and they were looking all over the place, and uh, about, eventually they came to notify my mother that I got lost. They saw me there and luckily everything ended up nice.

Fig. 2. Representative sample of a fictional event freely generated by K.C. (top) and by a control (bottom) in response to the childhood life period.

2004), K.C. had great difficulty generating fictional stories from any supposed time period in the free generation condition (data presented in Fig. 1; see Fig. 2 for sample narratives). Specifically, performance was significantly worse than that of controls for the three most remote time periods (childhood: $-2.32, p=0.05$; adolescence: $-2.26, p=0.05$; early adulthood: $-4.12, p=0.01$) and approached significance for the two most recent time periods (mid adulthood: $-2.04, p<0.07$; past year: $-1.93, p=0.07$). Qualitative ratings indicated a similar pattern, with significantly worse performance for all premorbid time periods (childhood: $-3.37, p=0.02$; adolescence: $-6.32, p=0.004$; early adulthood: $-2.34, p=0.05$; mid adulthood: $-6.5, p<0.004$) and a trend towards significance for the past year ($-1.76, p<0.09$). The number of details generated by K.C. increased with structured probing. However, performance remained significantly below control levels for all but the mid adulthood time period for quantitative analysis of internal details, which approached significance (childhood: $-3.92, p=0.01$; adolescence: $-2.4, p<0.05$; early adulthood: $-4.8, p<0.01$; mid adulthood: $-2.14, p=0.06$; past year: $-2.74, p<0.04$), and for all time periods when based on qualitative ratings (childhood: $-6.98, p=0.003$; adolescence: $-2.52, p<0.05$; early adulthood: $-8.94, p=0.001$; mid adulthood: $-6.71, p=0.003$; past year: $-9.69, p=0.001$). Analysis of external details yielded similar results for both free generation (childhood: $-1.62, ns$; adolescence: $-2.14, p=0.06$; early adulthood: $-1.74, p=0.09$; mid adulthood: $-1.5, ns$; past year: $-4.16, p=0.01$) and structured probing (childhood: $-1.38, ns$; adolescence: $-1.67, ns$; early adulthood: $-1.12, ns$; mid adulthood: $-1.82, p=0.08$; past year: $-3.25, p=0.02$).

Overall, K.C. was able to invent stories from beginning to end in response to event topics that were plausible, but the stories were without the richness in detail typical of the fictional incidents created by control participants. Nonetheless, unlike his inability to describe real-life events in a test of AM, what little was told was sequential in nature and seemed to possess a somewhat episodic flavour. Notwithstanding this, his fictional narratives lacked the contextual and perceptual qualities as well as semantic content to simulate complete personal reliving of each event (see Fig. 2).

1.3. Semantic narrative test

1.3.1. Procedure

K.C.'s impaired performance on the fictional event test suggests that his deficit may be exacerbated by, but is not limited to, a loss of episodic details. Moreover, preliminary testing using highly improbable occurrences (UFO visit, winning the lottery) yielded comparable results, suggesting that it is unlikely that K.C.'s impairment is due to reliance on actual past experiences. Thus, non-personal semantic narratives were used to test if his deficit occurs when binding is necessary for task performance, but when neither self-projection nor memory for event details is required.

1.3.1.1. Free recall. This semantic cue-word test required participants to retrieve details of commonly known complex semantic narratives (fairy tales and bible stories), which were acquired long before the onset of K.C.'s amnesia (Gilboa et al., 2006b). Participants were first asked to rate their familiarity with the following fairy tales and bible stories (using a Likert scale of 1 = vaguely familiar to 5 = very familiar): Little Red Riding Hood, Snow White, Jack and the Beanstalk, Hansel and Gretel, Moses and the Exodus, Noah's Ark, a Adam and Eve in the Garden of Eden. Participants then recounted the four narratives that they rated as most familiar and were prompted to provide as many details as possible. Responses were recorded, transcribed, and scored according to the total number of details (true details, errors, or repetitions) generated for each narrative. General prompting was used to encourage recall of as many details as possible ("can you remember anything else?" or "what else happened?"). If, despite their high rating, participants could not recall any detail of the story, a set of pre-determined cues, one per story, were used as prompts (e.g., 'If I tell you the word 'giant' can you recall anything from the story?'). Overall richness and coherence scores were derived from analyses of the narratives as follows:

- Richness score:** narratives were scored by segmenting the verbal output into informational bits (Gilboa et al., 2006b; Levine et al., 2002) and categorizing details into one of four categories: event details (ED), perceptual/description (P/D), repetitions, and meta-cognitive statements. ED was defined as any detail conveying essential information regarding the story (e.g., "Little Red Riding Hood met a wolf"), whereas P/D was defined as any detail conveying information that is not essential to the storyline but that adds information that is either perceptual in nature ("the castle was black"), or descriptive in a way that qualifies an ED but does not change the storyline ("the dwarfs were kindhearted"). Erroneous details were not omitted from the overall score as few errors were made and the focus of the study was the way a story is conveyed rather than its accuracy. Inter-rater agreement for 10 randomly selected narratives scored was 88%.
- Coherence score:** a coherence score was derived to capture how well a narrative conveyed the main themes of a story and whether it followed the correct order of events or was fragmented and patchy. To this end, each original story was divided into 12 main themes that constitute the storyline and numbered 1–12 based on the order of appearance. Themes were independently determined by two raters (R.S.R. and A.G.), with disagreements (which were fewer than 10%) resolved through discussion. To determine a coherence score, the number of themes appearing in each narrative was counted and their order of appearance was noted. One point was given for each theme that appeared later than its actual

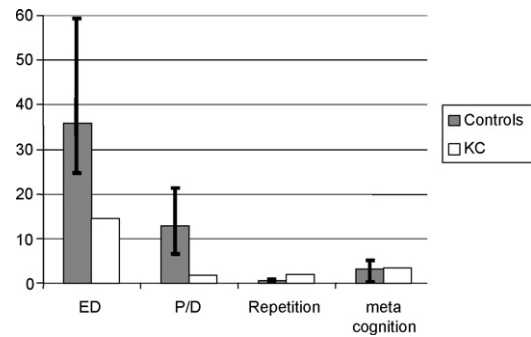


Fig. 3. Mean number of details by types generated per script by K.C. and healthy controls on free recall of semantic scripts. Error bars represent maximum and minimum scores by controls. ED, event detail; P/D, perception/description.

position in the storyline. (e.g., a thematic order of 2, 4, 5, 3, 6 was awarded 2 points because theme 3 appeared later than themes 4 and 5). This score was expressed as a ratio of the total themes generated for each narrative, with 0 expressing a correct order of themes and higher ratio expressing less coherent stories.

1.3.1.2. Recognition. A recognition version of this test was also administered to determine if K.C.'s performance was affected by a general difficulty in retrieval or verbal fluency. Participants were presented with the title of each of the four stories they recalled earlier on a computer monitor (Gilboa et al., 2006b). Forty sentences (half true and half false) that told the story in chronological order were presented one at a time on the screen, and participants were required to indicate with a button press if the sentence was correct. The title of the story appeared on the screen throughout, as did reminders of the mapping of the response keys. Participants had 10 s to respond to each sentence before it disappeared from the screen, though responses made after the time limit were also noted. Participants were required to rate their confidence level in judging the accuracy of each sentence (high or low) before proceeding to the next sentence. In a previous study, K.C. was administered a similar recognition test for 6 retrograde and 2 anterograde autobiographical events (Gilboa et al., 2006a), allowing for comparisons with his present performance.

1.3.2. Results

1.3.2.1. Recall. Fig. 3 presents the results of the free recall of semantic narratives for K.C. and the group of matched controls. K.C. showed severe deficits in generation of details for the narratives selected, producing on average 14.5 event details and only 1.75 perceptual/descriptive details, well below the range of controls, but not at floor. He had more repetitions, as would be expected given his memory impairment, and roughly the same number of meta-cognitive statements.

Coherence scores: Despite his poor performance in terms of richness of details, K.C.'s performance was within the lower bounds of the range of performance of controls, producing on average 5.25 themes per story out of 12 (controls: mean = 6.96; S.D. = 2.02; range = 4.5–10.5). However, his thematic coherence score, expressed as a ratio of the number of points scored for order deviation and the total number of themes, was much higher than controls' (controls: mean = 0.035; S.D. = 0.036). Whereas the controls' range on this ratio was 0–0.097, K.C.'s score was 0.285. Thus, despite relatively normal performance with regard to the number of themes produced, K.C.'s stories were disorganized and lacked coherence.

1.3.2.2. Recognition. On recognition of details pertaining to the semantic narratives, K.C. showed few deficits, if any (presented in Fig. 4). His hit rate was 0.84, equivalent to controls' lower range of 0.85. His false alarm rate, however, was 0.2, slightly higher than that of any of the other participants. Nonetheless, his overall performance indicates relatively intact discrimination ability.

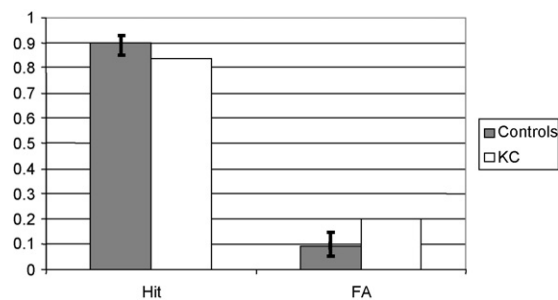


Fig. 4. Hit rate and false alarm rate (FA) for K.C. and controls on recognition of true and false details from semantic narratives. Error bars represent maximum and minimum scores by controls.

Taken together, the results of Experiment 1 were supported by a complementary finding of deficient recounting of fairy tales and bible stories from remote semantic memory at recall. However, the thematic elements of the stories at recall and identification of true from false details at recognition were intact. The demonstration of impaired performance when narratives have a pre-existing form, when the story details are maintained in storage, and when self-projection is not needed, suggests that K.C.'s amnesia entails more than a loss of information necessary for constructing elaborate and coherent descriptions. An additional reconstructive process is also faulty.

2. Discussion

This study addressed whether extensive remote memory loss specific to autobiographical information in amnesia is due to an inability to represent episodic details in long-term AM or to a more general construction deficit that does not permit generation or binding of details, independent of AM. K.C. had the most difficulty in reconstructing memories of events he experienced in the past, but he also was impaired in constructing from imagination detailed events that were never personally experienced, as well as non-personal semantic narratives that were learned many years prior to his injury. The findings suggest that an inability to access self-relevant, episodic details from memory, as well as difficulty in binding details into a coherent narrative structure, even when they were semantic in nature, both contribute to K.C.'s impaired AM. Though impaired overall on the latter two tasks, K.C. was able, nonetheless, to generate the gist and some details of personal and non-personal narratives. Moreover, tests of recognition of the elements of fairy tales and bible stories indicated that his knowledge of them was preserved. This preservation stands in stark contrast to his virtually non-existent AM (Rosenbaum et al., 2004, 2005) even when tested with recognition (Gilboa et al., 2006a).

There has been a recent surge of interest in the relation of episodic memory, and the structures that mediate it, to non-mnemonic abilities, such as imagination (e.g., Buckner & Carroll, 2007; Hassabis, Kumaran, & Maguire, 2007; Schacter et al., 2007; Suddendorf & Corballis, 2007; Tulving, 1985). Indeed, it is becoming apparent that the hippocampus, a structure that is critical to episodic memory, also may be involved in perception, imagination, and planning for the future, processes in which amnesic individuals are impaired (Graham et al., 2006; Hassabis, Kumaran, & Vann, et al., 2007; Klein et al., 2002; Lee et al., 2005; Moscovitch, 2008). These findings are consistent with recent neuroimaging evidence of a common neural substrate underlying AM and imagining of current or future events (Addis & Schacter, 2008; Addis, Wong, & Schacter, 2007; Hassabis, Kumaran, & Maguire, 2007; Szpunar, Watson, & McDermott, 2007). The current study extends these abilities to include imagined scenarios of premorbid personal life events as well as non-personal semantic narratives. K.C.'s generation of fictional event details appears to be severely deficient when his imagination is oriented to the past, as it is when oriented to the future (Tulving, 1985). Structured probing seemed to alleviate this deficit to some extent, but his performance was still significantly below that of controls for all imagined time periods.

K.C.'s inability to produce rich, coherent narratives, whether personal or non-personal, contrasts with his preserved knowledge of the gist of semantic narratives as reflected in his thematic score at recall, and his retained ability to identify true story details at recognition. This pattern of results may be understood better in the context of other areas of preservation and impairment exhibited by K.C. Previous investigations showed overall better performance for general semantic memory (Westmacott, Leach, Freedman, & Moscovitch, 2001) than for autobiographical episodic and personal semantic memory, both for recall (Rosenbaum et al., 2004) and recognition (Gilboa et al., 2006a). In an earlier study, we tested K.C. on a wide range of visual imagery tests to determine if it is a lack of visual imagery due to medial occipital damage that accounts for

his poor episodic memory performance (Rosenbaum et al., 2004). Not only was he able to comment on the appearance and spatial location of imagined objects, but he was also able to draw on this existing semantic knowledge to manipulate and recombine static images into new ones. K.C.'s amnesia could not be due entirely to a strategic retrieval deficit related to frontal lobe damage, as he did not benefit from structured probing during retrieval of past personal events as do other frontal patients with more basic retrieval problems (Levine, 2004). The latter was confirmed in a test of K.C.'s ability to distinguish details relating to events that he had experienced across his lifetime from those that he had never experienced on a recognition measure of AM (Gilboa et al., 2006a). Although the details invented were plausible in the context of the participants' lives, K.C. showed near-chance performance, whether the details were episodic, generic, or semantic in nature, whereas control participants had little difficulty distinguishing true from false details of any sort.

In the current study, K.C.'s performance on the fairy tale/bible story measure of non-personal narrative reconstruction fell somewhere between his generally intact semantic memory but impaired AM. The difference may be due to the dynamic quality of narratives in comparison to isolated semantic facts. However, it may also suggest that distinctions between detailed and schematic representations can exist within semantic memory for narratives, much like those identified in remote spatial memory based on studies with K.C. (Rosenbaum et al., 2000; Rosenbaum, Winocur, & Moscovitch, 2001). Indeed, previous work has demonstrated that allocentric relations among landmarks contained within old neighbourhoods are retained, whereas specific details that may be incidental to navigation, such as the visual identity of neighbourhood houses, are lost.

One possible explanation for this deficit is that there is a normal tendency to rely on true AM's when generating fictional details. This idea is captured by the "constructive-episodic-simulation hypothesis" recently proposed by Schacter and Addis (2007), which views future imagining as a simulation based on the reformulation of various event details from past personal experiences. If, however, participants must rely on their personal episodic memory to construct novel events, then K.C.'s retrieval of semantic narratives should have been within the control range. This was not the case, even when the information needed to construct the narratives was available to him. Moreover, as a further comparison, K.C. and a control participant were asked to construct fictional stories about events that were unlikely ever to have happened to them given life circumstances. Preliminary findings indicated that, unlike the control participant, K.C.'s narratives for implausible happenings were comparable to those for plausible happenings, making it unlikely that he unintentionally drew on personal experiences when instructed not to provide details of true episodes on the fictional event test. Thus, although the loss of episodic memories may exacerbate his condition, there are additional impairments that account for the full spectrum of his deficits.

A related hypothesis is that a process of self-projection is essential to both episodic remembering and imagining, and accounts for the high degree of overlap in the neural networks engaged across neuroimaging studies of these and related abilities (Buckner & Carroll, 2007). Insofar as ToM is related to self-projection, the evidence indicates that ToM and AM can be uncoupled. Although it shares with AM a neural substrate based on neuroimaging data (Buckner & Carroll, 2007), ToM appears to be preserved in K.C. despite his AM impairment (Rosenbaum et al., 2007). This finding indicates that AM can be impaired despite preserved self-projection and, conversely, that imagining others' thoughts does not depend on the ability to re-experience details of past episodes that are relevant to the other person's current situation.

Overall, two parallel deficits may be at work, one relating to missing bits of information that would normally lend to the richness of a narrative, and the other to the fragmented composition of those bits into a narrative that lacks coherence. This interpretation is in line with the one proposed by *Hassabis, Kumaran, and Vann, et al. (2007)* to account for the finding that amnesic patients are only able to envision fragmented images of commonplace scenes, such as a day at the beach. They believed that the scenes would encourage participants to draw on repeated past experiences (i.e., generic memories) rather than a single unique event. We, too, found that under more structured conditions, K.C. is capable of generating fragments, possibly due to basic associative processes, but even then he is unable to assemble those fragments into narratives that are rich in detail. Our paradigm did not include a measure of spatial coherence, but analyses based on detail type suggested that the sparseness of detail characteristic of K.C.'s narratives was not specific to the spatial domain, perhaps because participants were asked to construct plausible scenarios rather than scenes. Although the "scene construction" explanation remains viable, another alternative is that the online binding process itself is essential to dynamic narrative generation, in place of or in addition to the process of creating a spatial context in which details of narratives are bound. In that sense, the deficit may reflect, more generally, the breakdown of a common constructive process that is associated equally with AA and RA, as the relational-binding hypotheses would predict (*Eichenbaum, 2004; Eichenbaum et al., 1994; Ryan et al., 2000*).

We propose a novel application of a framework that treats 'detailed' and gist-like, 'schematic' representations as complementary systems that differ in terms of their underlying cognitive processes and neural circuitry, and that may partially apply to both memory and non-memory domains. This framework incorporates and extends aspects of Multiple Trace Theory (MTT) as advanced by *Nadel and Moscovitch (1997, 2001)*, but makes more specific predictions with respect to the fate of non-mnemonic representations in MTL and neocortical regions. What may be lost in AA and RA is the ability to generate detailed aspects of narratives, whether of real or imagined experiences or stories, although the gist is retained. It remains to be seen through studies of patients with focal AA or RA whether this process is identical for novel patterns of information as in AA and for re-activation of old ones as in RA.

Although K.C. has extensive bilateral damage to the hippocampus, he also has damage to other regions, preventing us from ascribing his deficits exclusively to hippocampal damage. Nevertheless, his deficits are consistent with those of other patients with hippocampal damage, both on these tasks and on others we conducted throughout the years (*Rosenbaum et al., 2005*). The hippocampus is needed to link together local elements that can be held as a unit in working memory (*Hannula & Ranganath, 2008; Ryan et al., 2000*). It is also needed to refer to recently constructed elements that are held in memory and may serve as indices of how much more detail needs to be added. This is an associative process. The various units are assembled by the prefrontal cortex so that the narrative makes sense at a global level. This is a more hierarchical process. It is significant in this regard that the overall structure of K.C.'s narratives is appropriate but that the local elements are faulty or poorly detailed.

In sum, the current results suggest that K.C.'s retrograde AM deficit reflects both loss of details from storage as well as an inability to bind together the few details that remain. Future investigation is needed to determine if both types of deficit arise in patients with more circumscribed lesions to the hippocampus and prefrontal cortex, and whether these deficits are distinct from those implicated in "scene construction" or contribute to them.

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References

- Addis, D. R., & Schacter, D. L. (2008). Constructive episodic simulation: Temporal distance and detail modulate of past and future events modulate hippocampal engagement. *Hippocampus, 18*, 227–237.
- Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia, 45*, 1363–1377.
- Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences, 11*, 9–57.
- Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology, 16*, 693–700.
- Dyer, J. R., Shatz, M., & Wellman, H. M. (2000). Young children's storybooks as a source of mental state information. *Cognitive Development, 15*, 17–37.
- Eichenbaum, H. (2004). Hippocampus: Cognitive processes and neural representations that underlie declarative memory. *Neuron, 44*, 109–120.
- Eichenbaum, H., Otto, T., & Cohen, N. J. (1994). Two functional components of the hippocampal memory system. *Behavioural Brain Sciences, 17*, 449–517.
- Gilboa, A., Alain, C., Stuss, D. T., Melo, B., Miller, S., & Moscovitch, M. (2006). Mechanisms of spontaneous confabulations: A strategic retrieval account. *Brain, 129*, 1399–1414.
- Gilboa, A., Winocur, G., Rosenbaum, R. S., Poreh, A., Gao, F., Black, S. E., Westmacott, R., & Moscovitch, M. (2006). Hippocampal contributions to recollection in retrograde and anterograde amnesia. *Hippocampus, 16*, 966–980.
- Graham, K. S., Scahill, V. L., Hornberger, M., Barense, M. D., Lee, A. C., Bussey, T. J., & Saksida, L. M. (2006). Abnormal categorization and perceptual learning in patients with hippocampal damage. *Journal of Neuroscience, 29*, 7547–7554.
- Hannula, D. E., & Ranganath, C. (2008). Medial temporal lobe activity predicts successful relational memory binding. *Journal of Neuroscience, 28*, 116–124.
- Hassabis, D., Kumaran, D., & Maguire, E. A. (2007). Using imagination to understand the neural basis of episodic memory. *Journal of Neuroscience, 27*, 14365–14374.
- Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *Proceedings of the National Academy of Sciences, 104*, 1726–1731.
- Klein, S. B., Loftus, J., & Kihlstrom, J. F. (2002). Memory and temporal experience: The effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. *Social Cognition, 20*, 353–379.
- Kopelman, M. D., Wilson, B. A., & Baddeley, A. D. (1990). *The autobiographical memory interview*. Suffolk, England: Thames Valley Test Company.
- Lee, A. C., Bussey, T. J., Murray, E. A., Saksida, L. M., Epstein, R. A., Kapur, N., Hodges, J. R., & Graham, K. S. (2005). Perceptual deficits in amnesia: Challenging the medial temporal lobe 'mnemonic' view. *Neuropsychologia, 43*, 1–11.
- Levine, B. (2004). Autobiographical memory and the self in time: Brain lesion effects, functional neuroanatomy, and lifespan development. *Brain and Cognition, 55*, 54–68.
- Levine, B., Svoboda, E., Hay, J. F., Winocur, G., & Moscovitch, M. (2002). Aging and autobiographical memory: Dissociating episodic from semantic retrieval. *Psychology of Aging, 17*, 677–689.
- Mar, R. A., & Oatley, K. (2008). The function of fiction is the abstraction and simulation of social experience. *Perspectives on Psychological Science, 3*, 173–192.
- Moscovitch, M. (2008). The hippocampus as a "stupid," domain-specific module: Implications for theories of recent and remote memory. *Canadian Journal of Experimental Psychology, 62*, 62–79.
- Nadel, L., & Moscovitch, M. (1997). Consolidation, retrograde amnesia and the hippocampal formation. *Current Opinion in Neurobiology, 7*, 217–227.
- Nadel, L., & Moscovitch, M. (2001). The hippocampal complex and long-term memory revisited. *Trends in Cognitive Sciences, 5*, 228–230.
- Rosenbaum, R. S., Köhler, S., Schacter, D. L., Moscovitch, M., Westmacott, R., Black, S. E., Gao, F., & Tulving, E. (2005). The case of K.C.: Contributions of a memory-impaired person to memory theory. *Neuropsychologia, 43*, 989–1021.
- Rosenbaum, R. S., McKinnon, M., Levine, B., & Moscovitch, M. (2003). Visual imagery or strategic retrieval: Disentangling the nature of patient K.C.'s autobiographical memory deficit. *Cognitive Neuroscience Society Abstracts, 10*, 36.
- Rosenbaum, R. S., McKinnon, M. C., Levine, B., & Moscovitch, M. (2004). Visual imagery deficits, impaired strategic retrieval, or memory loss: Disentangling the nature of an amnesic person's autobiographical memory deficit. *Neuropsychologia, 42*, 1619–1635.
- Rosenbaum, R. S., Priselac, S., Köhler, S., Black, S. E., Gao, F., Nadel, L., & Moscovitch, M. (2000). Remote spatial memory in an amnesic person with extensive bilateral hippocampal lesions. *Nature Neuroscience, 3*, 1044–1048.

- Rosenbaum, R. S., Stuss, D. T., Levine, B., & Tulving, E. (2007). Theory of mind is independent of episodic memory. *Science*, *318*, 1257.
- Rosenbaum, R. S., Winocur, G., & Moscovitch, M. (2001). New views on old memories: Re-evaluating the role of the hippocampal complex. *Behavioural Brain Research*, *127*, 183–197.
- Ryan, J. D., Althoff, R. R., Whitlow, S., & Cohen, N. J. (2000). Amnesia is a deficit in relational memory. *Psychological Science*, *11*, 454–461.
- Schacter, D. L. (1999). The seven sins of memory. Insights from psychology and cognitive neuroscience. *The American Psychologist*, *54*, 182–203.
- Schacter, D. L., & Addis, D. R. (2007). The cognitive neuroscience of constructive memory: Remembering the past and imagining the future. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *362*, 773–786.
- Schacter, D. L., Addis, D. R., & Buckner, R. (2007). Remembering the past to imagine the future: The prospective brain. *Nature Reviews Neuroscience*, *8*, 657–661.
- Schacter, D. L., Addis, D. R., & Buckner, R. (2008). Episodic simulation of future events: Concepts, data and applications. *Annals of the New York Academy of Sciences*.
- Suddendorf, T., & Corballis, M. C. (2007). The evolution of foresight: What is mental time travel and is it unique to humans? *Behavioral and Brain Sciences*, *30*, 299–351.
- Szpunar, K. K., Watson, J. M., & McDermott, K. B. (2007). Neural substrates of envisioning the future. *Proceedings of the National Academy of Sciences*, *104*, 642–647.
- Tulving, E. (1985). *Elements of episodic memory*. Oxford: Clarendon Press.
- Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review in Psychology*, *53*, 1–25.
- Tulving, E., Schacter, D. L., McLachlan, D. R., & Moscovitch, M. (1988). Priming of semantic autobiographical knowledge: A case study of retrograde amnesia. *Brain and Cognition*, *8*, 3–20.
- Westmacott, R., Leach, L., Freedman, M., & Moscovitch, M. (2001). Different patterns of autobiographical memory loss in semantic dementia and medial temporal lobe amnesia: A challenge to consolidation theory. *Neurocase*, *7*, 37–55.