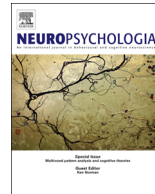




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Medial temporal and neocortical contributions to remote memory for semantic narratives: Evidence from amnesia

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ABSTRACT

Studies of remote memory for semantic facts and concepts suggest that hippocampal lesions lead to a temporally graded impairment that extends no more than ten years prior to the onset of amnesia. Such findings have led to the notion that once consolidated, semantic memories are represented neocortically and are no longer dependent on the hippocampus. Here, we examined the fate of well-established semantic narratives following medial temporal lobe (MTL) lesions. Seven amnesic patients, five with lesions restricted to the MTL and two with lesions extending into lateral temporal cortex (MTL+), were asked to recount fairy tales and bible stories that they rated as familiar. Narratives were scored for number and type of details, number of main thematic elements, and order in which the main thematic elements were recounted. In comparison to controls, patients with MTL lesions produced fewer details, but the number and order of main thematic elements generated was intact. By contrast, patients with MTL+ lesions showed a pervasive impairment, affecting not only the generation of details, but also the generation and ordering of main steps. These findings challenge the notion that, once consolidated, semantic memories are no longer dependent on the hippocampus for retrieval. Possible hippocampal contributions to the retrieval of detailed semantic narratives are discussed.

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1. Introduction

The study of remote memory in patients with medial temporal lobe (MTL) amnesia provides important insights into the nature of hippocampal-neocortical interactions supporting the formation of durable long-term memories. In recent years, much of this research has focused on the fate of episodic memories, in light of contradictory findings regarding the temporal extent and severity of episodic memory loss following hippocampal lesions. These findings have been leveraged as critical sources of support for competing theories of memory consolidation (Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Squire, 1992; Squire & Alvarez, 1995; Winocur & Moscovitch, 2011).

Less controversial has been the status of semantic memory following MTL lesions. Studies of remote memory for facts, public events, and personalities typically show either intact remote memory in patients with lesions restricted to the hippocampal region or retrograde amnesia extending at most 10 years (for review, see Fujii, Moscovitch, & Nadel, 2000; Moscovitch et al.,

2006; Winocur & Moscovitch, 2011), although there are exceptions finding a more extensive gradient (Cipolotti et al., 2001; Reed & Squire, 1998), possibly reflecting the fact that memory for public information can be aided by personal, episodic recollections in healthy participants (Westmacott, Black, Freedman, & Moscovitch, 2004). The temporally graded semantic memory loss in patients with hippocampal lesions stands in contrast to the much more extensive impairment seen in patients whose lesions involve surrounding neocortex (Fujii et al., 2000; Moscovitch et al., 2006; Squire & Bayley, 2007; Winocur & Moscovitch, 2011). These findings have been taken to suggest that the hippocampus has a time-limited role in semantic memory. That is, the hippocampus is thought to be critical for initially linking informational elements that are processed in disparate neocortical areas into coherent memories. With repeated re-activation of these hippocampal-neocortical interactions, linkages within a distributed neocortical network are strengthened, such that eventually memories can be retrieved without hippocampal mediation (Squire, 1992; Squire & Alvarez, 1995; Squire & Zola, 1998).

Neuropsychological studies exploring the role of the MTL in semantic memory have focused almost exclusively on memory for isolated elements of information. However, important information may also be gained from assessing memory for more complex semantic narratives that require the description of multiple

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semantic elements in their dynamic unfolding. [Moscovitch and Melo \(1997\)](#) were the first to examine memory for semantic narratives in amnesic patients. They asked a group of patients of mixed etiology to describe in detail historical events in response to a cue word, in a manner parallel to the method used to assess autobiographical memory. Although the primary focus of this study was on confabulation, non-confabulating amnesic patients were also impaired at describing historical events; in fact, their descriptions of historical events were no better than their descriptions of personal autobiographical events. More recently, [Rosenbaum, Gilboa, Levine, Winocur, and Moscovitch \(2009\)](#) assessed patient K.C.'s memory for fairy tales and bible stories, and similarly found that his narratives contained many fewer details than those of controls.

In both of these studies, the semantic knowledge was acquired long before onset of amnesia, and as such, the observed impairments stand in contrast to the findings of the semantic fact studies reviewed above, which typically found impairments restricted to knowledge acquired in the recent time period preceding the onset of amnesia. However, the implications of the findings from the narrative studies for the role of the MTL in semantic memory are unclear because the lesions in many of the amnesic patients under study included areas outside the MTL. In our own work ([Race, Keane, & Verfaellie, 2013](#)), we recently found that patients with lesions restricted to the MTL, while able to generate non-personal (semantic) issues that were significant in the past (e.g., "When you were growing up, what were the most important issues facing the environment?"), provided much less detail in elaborating on the impact of these issues. This impairment may be due to the demands on generative semantic memory that also characterize recall of historical events or fables. However, the impoverished retrieval of semantic information in amnesic participants in [Race et al. \(2013\)](#) could also have been due to the fact that such retrieval in control participants was facilitated by episodic memory processes involved in the recovery of autobiographical details (e.g., recalling being in a long line at the gas station when elaborating on the impact of oil shortages on people's lives), thus providing an alternative explanation for the impairment in amnesia.

The goal of the present study was to examine memory for well-established semantic narratives in patients with MTL amnesia. Like [Rosenbaum et al. \(2009\)](#), we turned to memory for fairy tales and bible stories because these stories are learned early in life, typically many years prior to the onset of amnesia, and their retrieval is not in any obvious way facilitated by autobiographical memory.

2. Methods

2.1. Participants

Eight patients with amnesia (two female) participated in the study. For each of these individuals, the neuropsychological profile indicated severe impairment limited to the domain of memory. Experimental data from one patient were excluded because she indicated low familiarity with all the stories, and as such, only the demographic and neuropsychological data for the remaining seven patients are presented in [Table 1](#).

Etiology of amnesia was ischemic or anoxic event in four patients, herpes encephalitis in two patients, and status epilepticus followed by temporal lobectomy in one patient. MRI/CT scans confirmed MTL pathology for five patients. Two could not be scanned because of medical contraindications (P04 and P05). MTL pathology for these patients was inferred based on etiology and neuropsychological profile. For two patients (P01 and P03), damage extended beyond the MTL to include anterolateral temporal neocortex. For one patient (P07) MRI was acquired in the acute phase of illness and there were no visible lesions on T1-weighted images. However, T2-flair images showed bilateral hyperintensities in the MTL and anterior insula. Patients' lesions are presented in [Fig. 1](#). As shown in [Table 1](#), volumetric data for the hippocampus and subhippocampal cortices using methodology reported

elsewhere ([Kan, Giovanello, Schnyer, Makris, & Verfaellie, 2007](#)) indicated that the lesion was restricted to the hippocampus in two patients (P02, P04).

Twenty healthy control subjects (13 female) who were matched to the amnesic group in terms of age (mean=56.9), education (mean=15.6), WAIS-III VIQ (mean=111.7) and Working Memory Index² (mean=107.9; all t 's < 1) also participated in the study. All participants provided informed consent in accordance with the Institutional Review Boards of Boston University and the VA Boston Healthcare System.

2.2. Materials

Five fairy tales and four bible stories were selected as narratives for the present study: Little Red Riding Hood, Hansel and Gretel, Goldilocks and the Three Bears, The Three Little Pigs, Cinderella, Moses and the Exodus, Noah's Ark, Adam and Eve, and The Nativity.

For each story, a recognition test was constructed that consisted of statements reflecting true details of the story (e.g. "The wolf arrives at the grandmother's house before Little Red Riding Hood") and statements incorporating two types of false details: inaccurate story details and story intrusions. Inaccurate details were story elements that were factually incorrect or described events that were the opposite of what actually happens in the story (e.g. "The wolf enters and poisons the grandmother before he eats her"). Story intrusions were details that occur in other popular narrative stories that were not part of the experiment (e.g. "Determined to reach the grandmother's house first, the wolf gives Little Red Riding Hood an enchanted apple that makes her fall asleep for a short while"). The recognition test for each story contained between 35 and 40 statements that told the story in chronological order. The average number of true details, inaccurate details, and story intrusions varied slightly across stories to ensure that all statements presented in chronological order formed a coherent narrative. Across stories, there were on average 19.3 true statements, 8.4 false statements containing inaccurate details, and 9.9 story intrusions.

2.3. Procedure

Participants were first presented with a list of the nine stories and were asked to rate their familiarity with each story using a Likert scale ranging from 1 (vaguely familiar) to 5 (very familiar). Subjects were then asked to indicate on a separate sheet their four most familiar stories. Memory was tested for the four stories that each participant selected as having the highest familiarity, provided a minimum familiarity rating of 3.³ This familiarity cut-off was set to ensure that poor memory was not a result of a lack of pre-morbid familiarity with the stories.

For the recall task, participants were asked to recount each story from beginning to end, as if the experimenter had never heard the story before. They were instructed to be as descriptive as possible, including as many details as they could recall. If a participant was unable to provide any accurate information about the narrative, a predetermined cue was given (e.g. for Little Red Riding Hood, the experimenter would prompt with, "If I say 'disguised wolf,' can you recall anything from the story?"). Participants were allowed to continue until their story reached its natural ending. At this point, the experimenter gave a general prompt (e.g. "Can you tell me anything else that happens in the story?"). If participants were able to provide additional details, they continued with their narrative until they indicated that they had finished.

For the recognition task, each narrative was presented on a computer screen, one statement at a time in sequential order, using E-Prime software. Participants were asked to state for each sentence whether it was true or false. The title of the narrative remained on the screen throughout the presentation of statements. Before beginning the recognition task, participants completed a practice session, consisting of eight sentences that described a scene from the popular movie "The Wizard of Oz." Half of the sentences were true and the remaining half were false and included both inaccurate details and story intrusions. Participants were asked to read each sentence out loud and to indicate whether they believed the sentence was true or false. Participants received feedback from the experimenter, and the different types of false statements were pointed out. When participants indicated that they understood the task, they continued with the test narratives. The experimenter recorded participant responses on a computer keyboard. No feedback was given during the recognition test.

Control participants completed recall and recognition for all four stories in a single session. For the amnesic patients, the task was broken up into multiple sessions to accommodate their slower pace and/or fatigue. Each session consisted of recall of one or more stories followed by recognition of the same stories.

² The Working Memory Index was prorated based on Digit Span and Arithmetic performance.

³ As noted in the subject section, this resulted in the elimination of an amnesic patient who indicated insufficient familiarity with any of the stories. In addition, only 3 stories met the set familiarity criterion for one control subject and 2 amnesic patients.

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