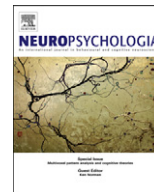




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Intact implicit verbal relational memory in medial temporal lobe amnesia

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ABSTRACT

To elucidate the role of the hippocampus in unaware relational memory, the present study examined the performance of amnesic patients with medial temporal lobe (MTL) lesions on a cued category-exemplar generation task. In contrast to a prior study in which amnesic patients showed impaired performance (Verfaellie et al., *Cognitive, Affective, and Behavioral Neuroscience*, 2006, 6, 91–101), the current study employed a task that required active processing of the context word at test. In this version of the task, amnesic patients, like control participants, showed enhanced category exemplar priming when the context word associated with the target at study was reinstated at test. The finding of intact implicit memory for novel associations following hippocampal lesions in a task that requires flexible use of retrieval cues is inconsistent with a relational memory view that suggests that the hippocampus is critical for all forms of relational memory, regardless of awareness. Instead, it suggests that unaware memory for within-domain associations does not require MTL mediation.

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1. Introduction

There is broad agreement that the hippocampus is critical for relational learning mechanisms that allow the rapid encoding of associations between different aspects of an event (Cohen & Eichenbaum, 1993; Eichenbaum, Yonelinas, & Ranganath, 2007; Henke, 2010). Such relational learning affords memories flexibility, in that the distinct elements and their interrelations can be retrieved through a variety of retrieval cues. This flexibility is an essential feature of declarative or explicit memory, and perhaps not surprisingly, much of the research characterizing the role of the hippocampus in relational memory has focused on explicit memory (Cohen & Eichenbaum, 1993; Eichenbaum & Cohen, 2001).

More controversial is the question as to whether the hippocampus also plays a role in the formation of relational representations that do not require conscious access (implicit memory). Several studies have reported impaired implicit memory in amnesia for visual scenes (Ryan, Althoff, Whitlow, & Cohen, 2000; Ryan & Cohen, 2004) or elements in a spatial array (Chun & Phelps, 1999), suggesting that the hippocampus is critical for relational memory even when the products of memory are unavailable to conscious awareness (Henke, 2010; Ryan & Cohen, 2003). However, this conclusion has been challenged on grounds that performance on these tasks may depend on

explicit memory (Smith, Hopkins, & Squire, 2006; Smith & Squire, 2008) or is impaired only when lesions extend beyond the hippocampus (Manns & Squire, 2001). From this perspective, it has been argued that the hippocampus does not contribute to unaware (implicit) relational memory.

This debate may be informed by studies of implicit memory for novel verbal associations in amnesia, i.e., the association between two words that do not have a pre-existing link. By the former (relational) view, amnesic patients should show impaired performance on such tasks, on the assumption that these tasks depend on the formation of flexible relational representations. By the latter view, amnesic patients should show normal performance on such tasks, as long as performance in control participants is not “contaminated” by explicit memory. The results of these sorts of studies have been mixed. Amnesic patients have shown intact implicit memory for novel associations on tasks such as perceptual identification (Gabrieli, Keane, Zarella, & Poldrack, 1997), lexical decision (Goshen-Gottstein, Moscovitch, & Melo, 2000), and word reading (Moscovitch, Winocur, & McLachlan, 1986), but impaired performance on a cued word stem completion task (Cermak, Bleich, & Blackford, 1988; Mayes & Gooding, 1989; Schacter & Graf, 1986b; Shimamura & Squire, 1989).

Based on this evidence, we previously postulated that the hippocampus might be critical for implicit memory for novel *conceptual*, but not *perceptual*, associations (Verfaellie & Keane, 2001, 2002). Priming for novel conceptual associations requires establishment of a meaningful relationship at study between two words that do not have a pre-existing semantic link (Schacter

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Table 1
Amnesic patient demographic and neurological characteristics.

Patient	Etiology	Age	Edu	WAIS, III	WMS, III				Volume z		
					VIQ	GM	VD	AD	WM	Hippoc.	Ant. parahipp.
P01	Encephalitis	54	14	92	45	56	55	85	-7.59	-.377	-1.74
P02	Encephalitis	65	12	106	69	68	77	111	-6.69	-5.03	-2.04
P03	Anoxia/Ischemia	59	12	83	52	56	55	91	N/A	N/A	N/A
P04	Pulmonary arrest	50	14	90	45	53	52	93	-7.54	-.59	.52
P05	CO poisoning	52	14	111	59	72	52	96	-2.35	-.54	1.46
P06	Encephalitis	80	18	135	45	53	58	141	N/A	N/A	N/A
P07	Cardiac arrest	56	17	134	70	75	67	126	N/A	N/A	N/A
P08	Ischemia	55	18	119	73	75	55	104	N/A	N/A	N/A
P09	Cardiac arrest	59	16	110	62	68	61	92	N/A	N/A	N/A

Note: Age=Age in years; Edu=Education in years; WAIS, III=Wechsler Adult Intelligence Scale, III; VIQ=Verbal IQ; WMS, III=Wechsler Memory Scale, III; GM=General Memory; VD=Visual Delayed; AD=Auditory Delayed; WM=Working Memory; Hipp.=Hippocampus; Ant. Parahipp.=Anterior Parahippocampus, which includes temporal pole, entorhinal, and perirhinal cortex; Post. Parahipp.=Posterior Parahippocampus.

& Graf, 1986a). If one supposes that implicit memory for novel conceptual (but not perceptual) associations requires the establishment of *flexible* relational representations, this account may be consistent with the relational view. Because evidence regarding the status of conceptual associative priming came from a single task, however, and because that task does not always yield reliable priming even in control subjects (Cermak et al., 1988), we explored this hypothesis further by examining amnesics' performance on two other conceptual associative priming tasks (Verfaellie, Martin, Page, Parks, & Keane, 2006). Consistent with our hypothesis, we found impaired associative priming in a cued category-exemplar task in which the reinstatement of contextual information associated with a target at study could enhance the likelihood of target generation at test. Importantly, performance on this task was dissociated from explicit memory in control participants, suggesting that the deficit in amnesia was truly one of unconscious memory. Inconsistent with our hypothesis, however, we found intact associative priming in a relatedness judgment task. These findings suggested that a simple perceptual/conceptual distinction could not account for the pattern of spared and impaired implicit associative memory in amnesia.

However, a relational memory account of our findings may be plausible in the context of closer consideration of the differences between these two conceptual associative tasks. One potentially important difference lies in the nature of the retrieval cues. In the relatedness judgment task, memory is tested using the exact retrieval cues that are present during learning (i.e., the two words are presented together in the study phase as well as in the test phase). In the category exemplar task, by contrast, a novel retrieval probe is presented at test. More specifically, whereas the context word and target word are presented together in the study phase (e.g., mall-rain), only the context word is presented at test together with a not previously seen category probe (e.g., mall-weather phenomena?). Thus, whereas associative priming on the relatedness judgment task can be mediated by unitized representations consisting of a rigid blend of the individual elements – representations that can be formed directly within neocortical regions (Goshen-Gottstein et al., 2000; Moses & Ryan, 2006) –, associative priming in the category exemplar task requires representational flexibility. As such, it can be argued that only performance on the exemplar task reflects true *relational* learning. Consequently, amnesics' failure to show associative priming in the category exemplar task might be taken as support for the notion that the hippocampus is critical for relational learning, regardless of whether those memories are accessible to awareness.

Before accepting this interpretation, however, it is important to consider another possible reason for the discrepancy in

amnesics' performance in the two conceptual associative priming tasks. In the relatedness judgment task, processing of the first word is mandatory, whereas in the category exemplar task, processing of the first word of the pair (the context word) is incidental to the task. Amnesics' impaired implicit associative memory in the latter task might be due to a failure to process the context word spontaneously (Verfaellie et al., 2006).

To provide further evidence regarding the role of the hippocampus in implicit relational memory, the current study examined the performance of patients with MTL amnesia on a cued category-exemplar task in which processing of the context word was mandatory. As outlined above, a critical feature of the task is that the retrieval probes at test are not present during study. This ensures that memory is mediated by the formation of a relational representation in which the individual components are maintained, rather than by a rigid, unitized representation. If amnesic patients show impaired associative priming in this task, it would provide critical evidence that the hippocampus is essential for unaware relational memory. Alternatively, if amnesic patients show intact associative priming in this task, it would suggest that some forms of relational representation can be established without hippocampal mediation.

2. Methods

2.1. Participants

Nine MTL-amnesic patients (4 female) and 18 healthy controls (15 female) participated in this study¹. The neuropsychological profiles of all patients indicated severe impairment limited to the domain of memory (see Table 1). The control group was matched to the amnesic group in terms of age (mean=64 years), education (mean=15 years), and WAIS-III Verbal IQ (mean=107.1; all $ts < 1$).

Etiology of amnesia was herpes encephalitis in three patients and ischemic or anoxic event in six patients. MR/CT scans confirmed medial temporal lobe pathology for all but two patients (P07 and P09) who could not be scanned because they had a pacemaker. For these patients, MTL pathology was inferred on the basis of etiology and neuropsychological profile. Of the patients who were scanned, six had visible lesions and one had reduced hippocampal size, but no visible lesion (P08). Lesion reconstruction overlays are presented in Fig. 1. Volumetric data were available for four patients (for details of volumetric analysis, see Kan, Giovanello, Schnyer, Makris, & Verfaellie, 2007). Two of these patients showed volume reductions (> 2 SD below the mean of eight age- and gender-matched controls subjects) limited to the hippocampus (P04 and P05), and two had volume reductions in the hippocampus and surrounding parahippocampal gyrus (see Table 1). The hippocampus was the only structure damaged in all patients and no common volume reductions were found outside the MTL.

¹ One patient was available for the implicit task, but not for the explicit task.

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