

Verbal recall in amnesia: Does scene construction matter?

Daniela J. Palombo^a, Dominoe Jones^b, Caroline Strang^b, Mieke Verfaellie^{b,c,*}

^a University of British Columbia, Department of Psychology, Canada

^b Memory Disorders Research Center, VA Boston Healthcare System, USA

^c Boston University School of Medicine, Department of Psychiatry, USA

ARTICLE INFO

Keywords:

Amnesia

Episodic memory

Hippocampus

Imagery

Medial temporal lobes

Scenes

ABSTRACT

The hippocampus plays a critical role in episodic memory and imagination. One theoretical model posits that the hippocampus is important for scene construction, namely, the ability to conjure and maintain a scene-based representation in one's mind. To test one idea put forth by this view, we examined whether amnesia is associated with more severe impairment in memory when the to-be-remembered content places high demands on scene construction. To do so, we examined free recall performance for abstract (i.e., low scene imagery) and concrete, high scene-imagery single words in seven amnesic patients with hippocampal lesions and concomitant scene-construction deficits, and compared their performance to demographically matched healthy controls. As expected, amnesic patients were severely impaired in their free recall performance; however, their impairment did not differ as a function of word type. That is, their impairment was equally severe for words that evoke high versus low scene imagery. These findings suggest that the role of the hippocampus in verbal memory extends to content that does not place high demands on scene construction. Theoretical implications of these findings are discussed.

1. Introduction

A critical role of the hippocampus in episodic memory is well established (e.g., Scoville and Milner, 1957). However, the precise role of this structure has been a hotly debated topic for decades, with a number of theories put forth in the literature (e.g., Graham et al., 2010; Cohen and Eichenbaum, 1993; Ryan et al., 2000; Schacter and Addis, 2007; Ekstrom and Ranganath, 2017; O'Keefe and Nadel, 1978). One such theory suggests that the hippocampus is important for scene construction. Scene construction refers to the ability to conjure and maintain in one's mind a scene, that is, a three-dimensional, spatially coherent representation that consists of objects viewed from an egocentric vantage point (e.g., Hassabis and Maguire, 2007; Dalton et al., 2018; also see Murray et al., 2018). By this view, the role of the hippocampus in episodic memory reflects the fact that such memories inevitably play out in a scene context.

The scene construction hypothesis was inspired, in part, by the observation that patients with hippocampal damage have difficulty constructing scenes even when imagining hypothetical events (Hassabis et al., 2007; also see Mullally et al., 2012), whereas they do not have difficulty imaging singular objects devoid of a spatial frame (e.g.,

Rosenbaum et al., 2004). Other work has shown a dissociation in performance between scene (relative impairment) and non-scene stimuli (relative sparing) in individuals with hippocampal amnesia both outside (e.g., Graham et al., 2006; Hartley et al., 2007; but see Kim et al., 2015) and within long-term memory (e.g., Lynch et al., 2020; Cipolotti et al., 2006; Bird et al., 2008). Further, neuroimaging work using fMRI shows that the hippocampus is more strongly engaged in tasks that have a high versus low scene demand (e.g., Palombo et al., 2018; Ross et al., 2018; Zeidman et al., 2015; Hodgetts et al., 2016; Robin et al., 2018; Hoscheidt et al., 2010; Bird et al., 2010), although it is important to note that some of this literature can be construed in terms of differences in relational processing demands, to which the hippocampus is also sensitive and upon which scene construction is reliant (see e.g., Roberts et al., 2018).

In apparent contradiction to the notion that the fundamental role of the hippocampus is one of scene construction, patients with amnesia, under some circumstances, show deficits in tasks with no obvious scene demands. For example, patients have trouble learning and remembering lists of words, e.g., in the context of verbal paired associates (VPA; Zola-Morgan et al., 1986; Shimamura and Squire, 1986), a finding that is more consistent with a prominent relational view of hippocampal functioning (see Cohen and Eichenbaum, 1993; Eichenbaum and Cohen,

* Corresponding author. Memory Disorders Research Center (MDRC 182), VA Boston Healthcare System, 150 S Huntington Avenue, Boston, MA, 02130, USA.

E-mail address: Mieke.Verfaellie@va.gov (M. Verfaellie).

2014; also see Konkel et al., 2008). Addressing this potential inconsistency with a scene construction account, Clark et al. (2018) surmised that VPA deficits in amnesia result from covert demands placed on scene imagery in such tasks (also see Maguire and Mullally, 2013). That is, many VPA tasks consist of concrete, highly imageable word pairs which may lend themselves to the use of visual imagery, in spite of the task being ‘verbal’ in nature (Clark et al., 2020; Clark and Maguire, 2016; also see Paivio et al., 1968).¹

To shed light on this issue, Clark et al. (2018) conducted an fMRI study, wherein they examined hippocampal engagement under three conditions. Participants learned and remembered word pairs, with the pairs including words that elicited scene imagery, words that elicited object imagery, or low imagery abstract words (i.e., words that represent concepts or ideas); the words were otherwise well matched on confounding characteristics and the conditions were designed to equate relational demands. The authors found that hippocampal engagement was present for scene and object pairs—with the strongest engagement for scene pairs—and absent for abstract word pairs (in comparison to single abstract words) even when restricting analyses to remembered pairs only (also see somewhat related work by Caplan and Madan, 2016; Klaver et al., 2005). Recruitment of the hippocampus for the object pairs was expected, given that two objects could draw on scene imagery, albeit less so than scene pairs. Together, these data seem to align with a scene-construction view of the role of the hippocampus in memory.

Critically, the findings of Clark and Maguire (2016) provide an explanation for the VPA deficits observed in amnesia. Moreover, they lead to the prediction that, all other factors held constant, amnesic patients with hippocampal damage would show a disproportionate deficit in memory for words that elicit high versus low imagery, especially when scene-based. Yet, no analogous amnesia study has been published to date. Older work in patients with temporal lobectomy (Jones-Gotman, 1979) showed that patients with sizable right-lateralized hippocampal lesions (versus patients with subtle hippocampal damage) had impaired incidental memory for word pairs following imagination instructions (especially when pairs consisted of concrete words), but the diagnosis of epilepsy makes interpretation of these findings somewhat difficult (also see Jones-Gotman and Milner, 1978). Another study showed that aging, which is typically associated with loss of hippocampal tissue, leads to a greater decline in episodic recollection for concrete versus abstract words (Peters and Daum, 2008). Note though that neither of these studies focused on scene imagery per se.

To fill this gap in the literature, in the present study, we compared a group of amnesic patients with hippocampal lesions and concomitant scene-construction deficits (Lynch et al., 2020) to healthy controls on a verbal memory task involving words that were either high in eliciting scene imagery or low in any form of imagery at all (i.e., abstract words). In our study, we opted to use single words rather than word pairs. Our rationale was that amnesic patients are impaired on verbal recall tasks even when their memory is assessed for single words (e.g., Rey Auditory Verbal Learning Test; Shimamura and Squire, 1986), and indeed this is the case for the patients included in our study. Our approach reduces task complexity and also reduces relational demands, relative to VPA tasks. To provide a strong psychometric assessment, we adjusted list length across conditions in order to performance-match scene and abstract word recall in healthy controls and compared control performance to that of the amnesic patients. In doing so, we eliminated the problem of comparing the magnitude of impairment across different levels of

overall performance in the two groups.

If the role of the hippocampus in memory reflects its contribution to scene construction, we should observe disproportionate impairment in the scene versus abstract word condition (i.e., a *condition by group* interaction). If, instead, the hippocampus is critical for mnemonic processes irrespective of demands on scene construction, we should observe equal impairment across the scene and abstract word conditions (i.e., only a main effect of *group*).

2. Method

2.1. Participants

Seven amnesic patients (one female) with medial temporal lobe (MTL) damage participated in this study. Etiologies of memory impairment included hypoxic-ischemic injury ($n = 4$), status epilepticus

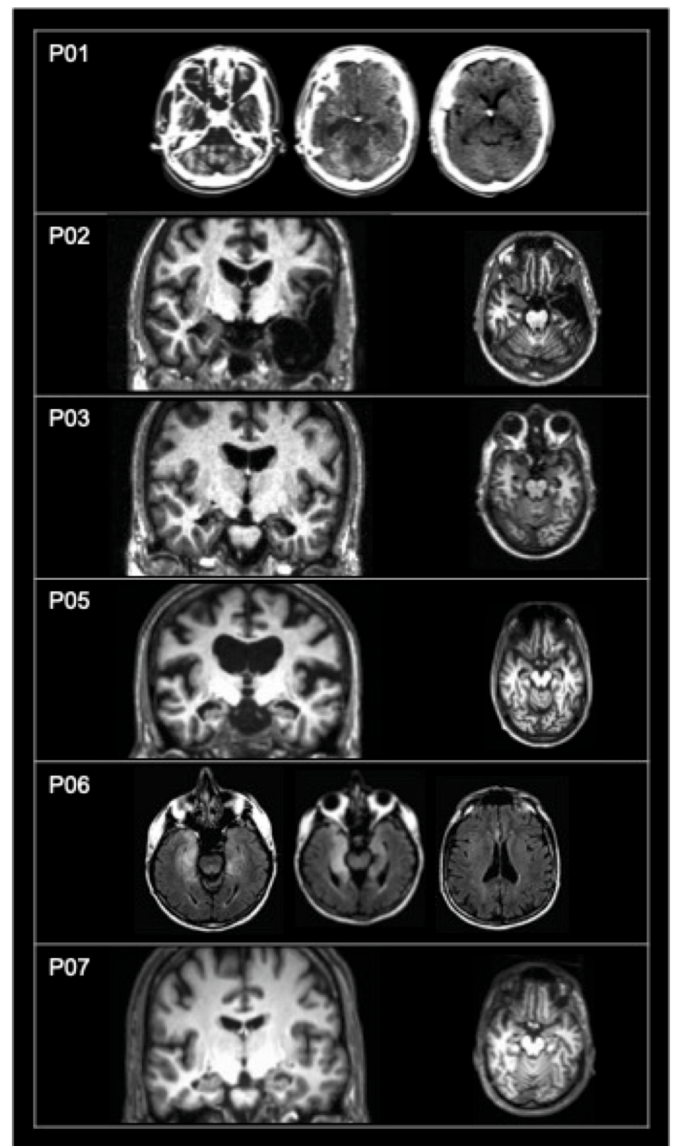


Fig. 1. Patient Scans.

Note. Structural MRI or CT scans depicting medial temporal lobe (MTL) lesions for 6 of the 7 amnesic participants. The left side of the brain is shown on the right side of the image. CT slices show lesion location for P1 in the axial plane. T1-weighted MRI images depict lesions for P2, P3, P5, and P7 in the coronal and axial plane. T2-flair MRI images depict lesion locations for P6 in the axial plane.

¹ Contrary to imagery-based theories, it has been argued that concreteness effects may be due to differential ‘context availability’ (i.e., information from one’s external or inner environment, including prior knowledge), which is thought to be higher for concrete versus abstract stimuli. Yet, when context availability is controlled for, the concreteness advantage in memory is not eliminated, suggesting that context availability cannot account for superior memory for concrete compared to abstract words (Schwanenflugel et al., 1992).

followed by left temporal lobectomy ($n = 1$), stroke ($n = 1$), and herpes encephalitis ($n = 1$). Lesions for 6 of the 7 patients are presented in Fig. 1, as either MRI or CT images. P04 could not be scanned due to medical contraindications and his MTL pathology was inferred from his etiology and neuropsychological profile.

Of the patients with available scans, one patient (P03) had MTL lesions restricted to the hippocampus and no other damage within extra-hippocampal MTL regions or outside of the MTL; two (P05 and P07) had lesions that included the hippocampus as well as amygdala, with damage in P05 extending into basal ganglia regions but no other extra-hippocampal MTL damage; one patient (P01) had a lesion that included the hippocampus and MTL cortices; and one patient (P02) had a lesion that extended well beyond the medial portion of the temporal lobes into anterior neocortex (due to temporal lobectomy). For the patient whose etiology was encephalitis (P06), clinical MRI was acquired only in the acute phase of the illness, with no visible lesions observed on T1-weighted images. However, T2-flair images demonstrated bilateral hyperintensities in the hippocampus and MTL cortices as well as the anterior insula. Volumetric data for the hippocampus and MTL cortices were available for four of the seven patients (P02, P03, P05, and P07; see Table 1), using methodology reported elsewhere (Kan et al., 2007).

Twenty-one healthy individuals (4 female; 17 male) without any self-reported neurological or psychological conditions participated as the control group in the study. These participants were matched for age ($M = 62.67$, $SD = 7.77$), education ($M = 15.55$, $SD = 2.70$), and verbal IQ ($M = 108.19$, $SD = 12.25$) to the participants with amnesia. No participants were excluded. All participants provided informed consent in accordance with the Institutional Review Board at VA Boston Healthcare System.

2.2. Materials

The stimuli consisted of 21 abstract words (mean concreteness = 1.82, $SD = 0.27$) and 30 scene words (mean concreteness = 4.61, $SD = 0.22$). The words and ratings of concreteness were taken from the Clark et al. study (2018). The words were divided into three paired lists of 7 abstract words and 10 scene words, which were matched for word frequency, age of acquisition, valence, arousal, length, and number of syllables, phonemes, orthographic neighbors, phonological neighbors with and without homophones, and phonographic neighbors with and without homophones (see Table S1). The normative ratings for the words were collected from The English Lexicon Project (Balota et al., 2007).

We pilot-tested 10 older adults (5 female; 5 male; mean age = 65.70, $SD = 7.39$) using abstract word lists of different lengths to determine the list length that elicited recall equivalent to that obtained for lists of 10 scene words. We found that this was accomplished by using lists of 7 abstract words, which is what was used in the actual experiment.

Table 1
Demographic, neuropsychological and neurological characteristics of amnesic patients.

Patients	Etiology	Age	Edu	WAIS III		WMS III			Volume Loss (%)			
				VIQ	WMI	GM	VD	AD	L Hipp	R Hipp	Total Hipp	Subhipp
P01	Hypoxic - ischemic	71	12	88	75	52	56	55	N/A	N/A	N/A	N/A
P02	Status epilepticus + left temporal lobectomy	58	16	93	94	49	53	52	89%	37%	63%	60% ^a
P03	Hypoxic - ischemic	65	14	106	115	59	72	52	18%	27%	22%	–
P04	Hypoxic - ischemic	69	17	131	126	86	78	86	N/A	N/A	N/A	N/A
P05	Hypoxic - ischemic	53	12	103	95	59	68	55	45%	46%	46%	–
P06	Herpes simplex encephalitis	79	13	99	104	49	56	58	N/A	N/A	N/A	N/A
P07	Stroke	56	20	111	99	60	65	58	46%	43%	43%	–
	Mean	64.43	14.86	104.43	101.14	59.14	64	59.43				
	SD	9.31	2.97	14.05	16.3	12.77	9.36	11.97				

Note. Age = age in years; Edu = education in years; WAIS-III = Wechsler Adult Intelligence Scale–Third Edition; WMS-III = Wechsler Memory Scale–Third Edition; VIQ = verbal intelligence quotient; WMI = working memory index; GM = general memory; VD = auditory delayed; AD = auditory delayed; L = left; R = Right; Hipp = hippocampus; Subhipp = sub-hippocampal cortices; N/A = not available. ^aVolume loss in left hemisphere, including anterior parahippocampal gyrus (i.e., entorhinal cortex, medial portion of the temporal pole, and the medial portion of perirhinal cortex; see Kan et al., 2007, for methodology).

Indeed, in the experiment (see below), performance in these conditions was well matched in healthy controls. Importantly, performance in healthy controls was below ceiling, eliminating the possibility that the magnitude of patients' impairment might be underestimated and differential impairment in one of the conditions might be masked.

2.3. Design and procedure

The order of presentation was counterbalanced between and within the three pairs of lists resulting in 12 counterbalances. Paired lists were always presented one after the other and the presentation of abstract (A) and scene (S) lists was alternated in an AS-SA-AS pattern. The order of the words within each list was also randomized (see Fig. 2).

Participants were shown a list of words on a computer screen, which they were asked to read out loud. Their goal was to try to remember as many words as they could at the end of the presentation. Each word was shown on the screen for 2.5 s followed by a 2 s fixation cross. Each list of words was shown twice with a short pause of about 10 s between the presentations. After the second presentation, participants counted backwards by 2 for 30 s before being asked to recall the words from the preceding list.

Participants were given a distractor task after every two lists where they were asked to rate the pleasantness of abstract paintings for about 6 min. Control participants completed all six of the word lists in one session whereas amnesic patients completed four lists in one session and two lists in a separate session to avoid fatigue. Additionally, amnesic patients completed the entire task a second time at least 80 days after the first administration and their performance was averaged across sessions. One patient was only tested once due to scheduling difficulty.

Due to COVID-19, 10 control participants were administered the task remotely and the remaining 11 control subjects were run in person. There were no significant differences in performance as a result of testing venue (abstract: $p = .40$; scene: $p = .77$). With the exception of three patients who participated remotely in one or two sessions, all patients were run in person. The remote testing was administered through screenleap.com which allowed participants to see the testing screen on their own device; they simultaneously communicated with the researcher over the phone. All participants confirmed they could adequately read the words on their screen before beginning the task. To make the administration as similar as possible, both the in person and remote participants were shown the stimuli through a timed PowerPoint task. Participants were told not to write down words.

3. Results

3.1. Patients versus controls

The average percentage of words recalled by word type is presented

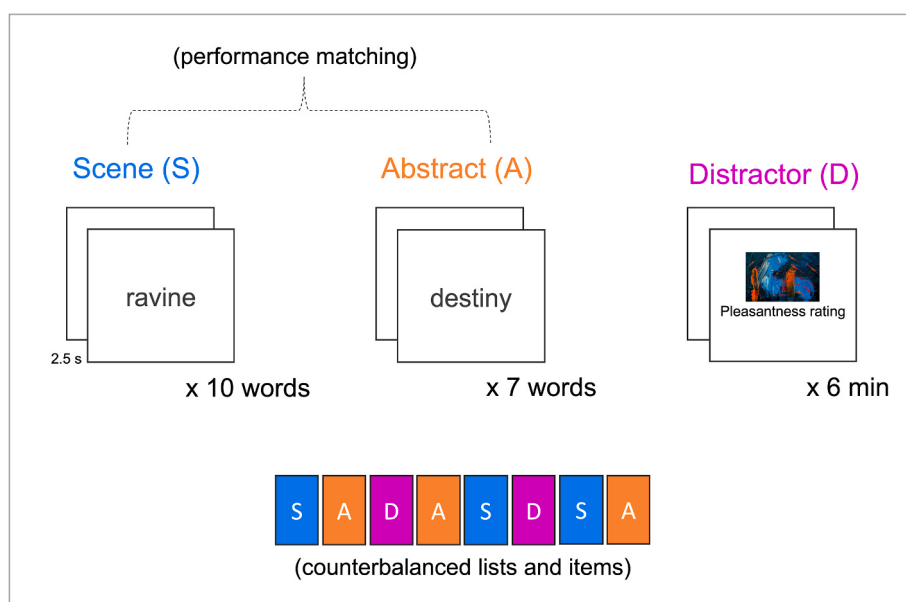


Fig. 2. Free recall task.

Note. Overview of the task design, including counterbalancing and performance matching. A distractor task was used to separate sets of lists to provide a break to participants.

in Table 2 (and additionally separated by list in Table S3). Given the proportional nature of the data, all analyses were run on arcsine transformed data. Analyses were run in JASP (JASP Team, 2022; Version 0.16.3). To examine whether patients with MTL damage differed in their ability to recall abstract and scene words when compared to controls, we conducted a 2 (Group) $\times$ 2 (Word Type) mixed-model ANOVA. This analysis yielded a main effect of Group ($F(1,26) = 38.250, p < .001, \eta_p^2 = 0.544$) but no effect of Word Type ($F(1,26) = 0.991, p = .329, \eta_p^2 = 0.003$) nor a significant interaction between Group and Word Type ($F(1,26) = 0.037, p = .849, \eta_p^2 = 1.178e-4$; see Fig. 3). In both conditions the impairment was so striking, that there was almost no overlap in the control and patient distributions (apart from one control participant's performance in the abstract condition, which fell within the patient group's distribution). A Bayesian mixed-model ANOVA showed that the data were 6.101 times more likely under the Group-only (best) model versus the model that included the Group $\times$ Condition interaction.

3.1.1. Patients versus controls, corrected for norming

We originally selected our words based on norms provided in Clark et al. (2018). However, a criticism of this approach is that their norming

Table 2

Percentage of free recall for abstract and scene words in individual amnesic patients and averaged across amnesic patients and controls.

	Full Stimulus Set		High Consensus Set	
	Abstract	Scene	Abstract	Scene
P01	38.10	36.67	32.38	39.44
P02	38.10	30.00	32.86	28.61
P03 ^a	35.71	25.00	36.19	26.16
P04	35.71	30.00	34.29	31.94
P05 ^a	4.76	10.00	5.71	9.35
P06	21.43	13.33	15.71	13.47
P07 ^a	11.90	18.33	14.76	18.43
Patient Mean	26.53	23.33	24.56	23.92
Patient SD	13.84	9.77	12.17	10.68
Control Mean	58.73	57.62	58.19	56.35
Control SD	16.24	8.95	17.76	8.29

Note. The data shown in the table are not transformed.

^a Refers to patients with damage restricted to the hippocampus within the medial temporal lobes.

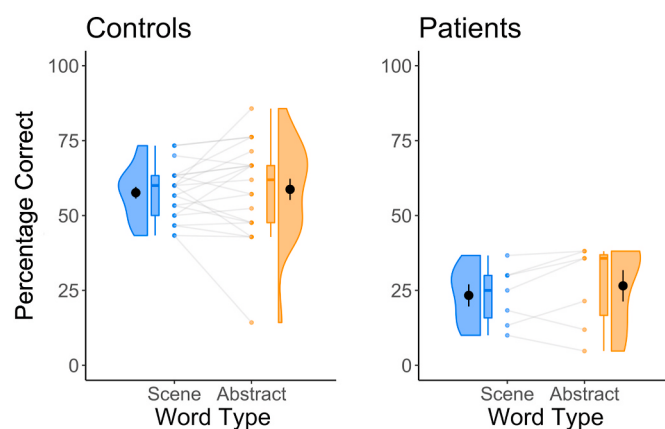


Fig. 3. Free recall performance.

Note. Raincloud plots depicting performance in healthy controls and amnesic participants.

was done in a different demographic (demographic information not reported in Clark et al. (2018)) and it is possible that ratings of scene imagery could differ in a sample within the age range of our healthy controls and patients. Hence, we conducted independent norming in a demographically matched sample, to assess whether the words differed in scene imagery as expected. The details of the norming are provided in Supplementary Materials. Our norming revealed strong overlap with Clark et al. (2018), however, 4 out of 21 words in the Abstract condition and 3 out of 30 words in the Scene condition did not meet our norming cutoff of 70% (see Appendix; also see Table 2). As such, we re-ran our analyses comparing amnesic patients versus controls with those words excluded from the analysis. The pattern of results did not change.

4. Discussion

In the present study, we investigated the role of the hippocampus in episodic memory for content associated with high versus low scene imagery. As expected, amnesic patients were severely impaired in their free recall performance; critically, however, their impairment did not

differ as a function of word type. That is, they were equally impaired in their free recall of words evoking low versus high scene imagery. Our findings show that amnesia does not always confer greater memory impairment for scene-based content.

Notably, the same pattern of results was observed in the subgroup of patients with MTL damage restricted to the hippocampus (see Table 2). This is relevant because some studies show that dissociations in memory for scene versus non-scene content are observed only in patients with focal hippocampal damage, devoid of damage to surrounding MTL cortices (e.g., Taylor et al., 2007; Bird et al., 2007). Interestingly, we do observe a selective scene deficit in some tasks in our patient group. For example, we recently showed that these patients are selectively impaired in a semantic task that places high demands on scene construction, whereas patients perform normally when scene demands are low (Lynch et al., 2020). Given these observations, it is unlikely that our failure to find disproportionate impairment in scene word recall in the present study is due to the lesion profile of these patients. However, it will be useful to replicate our results in a larger group of patients with focal hippocampal lesions.

Given the striking dissociation observed in Clark et al. (2018), wherein hippocampal activation was restricted to memory for word pairs high in scene construction, our findings are surprising. To our knowledge the study by Clark et al. (2018) is the only one to directly compare hippocampal involvement in scenes versus abstract words. Other neuroimaging studies have investigated concrete versus abstract words, with mixed results (e.g., see Caplan and Madan, 2016; Klaver et al., 2005; Fliessbach et al., 2006; Jessen et al., 2000; Fletcher et al., 1996), but these studies do not necessarily shed light on the scene construction theory as it is not known whether concrete words in these studies elicited scene or object imagery. Albeit in the context of word pairs, Clark et al. (2018) showed that hippocampal activation is greater for scene pairs versus object pairs; thus, mixed findings in prior studies might reflect greater use of scene imagery in some studies and greater use of object imagery in others. Notably, neuroimaging studies (including Clark et al., 2018) are correlational and thus leave open the question as to the causal role of the hippocampus in episodic memory for high versus low scene content.

It is important to highlight a methodological difference between our study and that of Clark et al. (2018), in that we used single words whereas Clark et al. (2018) used word pairs. This raises the possibility that the scene construction demands associated with remembering single words are fundamentally different from those associated with word pairs. For single words, it may be possible to draw on pre-existing scene representations, whereas word pairs require the integration of two unrelated elements into a novel scene. Yet, evidence from prior studies of patients with hippocampal damage who show deficits in certain remote spatial memory tasks—particularly those that seem to require detailed scene imagery (e.g., Rosenbaum et al., 2000; Maguire et al., 2006)—suggests that retrieval of remote scenes requires hippocampal (re)construction in a manner similar to the construction of new scenes (see Barry and Maguire, 2019), making this argument unlikely. Alternatively, it may be that the demands on scene construction, albeit qualitatively similar, are higher when thinking about scene pairs (wherein one needs to represent two scenes at once) versus conjuring a scene in relation to a single word. Future work should replicate our findings using word pairs.

In considering possible explanations for our results, we first considered the role of relational binding. We preface this by emphasizing that the scene construction theory is a relational theory, but posits that the hippocampus performs relational processing specifically *in the service of* building scenes. By contrast, other important theories postulate a more general role of the hippocampus in relational processing, namely, one that includes but is not limited to scenes (e.g., Konkel and Cohen, 2009; Cohen and Eichenbaum, 1993; Eichenbaum and Cohen, 2014; Ryan et al., 2000; also see Schacter and Addis, 2007; Roberts et al., 2018). Could the equivalent impairment for scene and abstract words in

amnesic patients be due to general demands on relational processing imposed by our task? On the one hand, we used single words as memoranda to minimize relational demands in our task. On the other hand, it could be that *any* relational demands elicited by the task precluded strong memory performance in amnesic patients. Indeed, in our prior work involving an overlapping group of amnesics, we used computational modeling to show that, whereas controls tend to temporally cluster their free recall of words—presumably by binding items to their evolving temporal context—patients do not (Palombo et al., 2019). That is, patients are less able to recover temporal context (i.e., relational) information that supports word recall (also see Howard et al., 2015). We note though that in Palombo et al. (2019), we did not manipulate imagery and all the words in the stimulus set were high in concreteness. Suggesting that contextual binding occurs regardless of the nature of the stimuli, Caplan and Madan (2016) showed no effect of imageability on temporal contiguity. Together with our data, these findings suggest that non-spatial relational binding may play an important role in free recall tasks. In the present study, although scene (and even object) imagery was negligible in the abstract condition (per our norming study; also see Clark et al., 2020), participants reported a high percentage of verbal thoughts (48% in the norming study). Such verbal thoughts can provide source context for retrieval, in that retrieval of the verbal thought provides a cue for the to-be-remembered information, in accordance with ideas from the temporal context model (Polyn et al., 2009). For example, when encoding the word *envy*, a participant may conjure an associated thought about an envious friend; this relational information can serve as context that facilitates later retrieval (also see Palombo et al., 2019). Such relational processing might be recruited more readily in open ended and difficult mnemonic tasks such as free recall compared to mnemonic tasks with more scaffolding (e.g., recognition memory), although more work will be needed to shed light on this.

Another, not mutually exclusive, possibility is that the hippocampus supports multiple cognitive processes, including both scene construction and *other* forms of relational processing. Compelling evidence comes from work by Dalton et al. (2018), who showed that different subregions within the hippocampus were differentially recruited for scenes versus non-scene relational processing. A portion of the anterior medial hippocampus encompassing pre/parasubiculum was preferentially recruited during scene construction (also see Dalton and Maguire, 2017; Ryan et al., 2010), whereas constructing an array (drawing equally on relational processes but without strong scene construction demands) engaged posterior hippocampus and a region localized to entorhinal cortex abutting the anterior portion of hippocampus but more anterior to the region recruited in scene construction. A similar location was also recruited for object triplets, devoid of spatial context, as was a cluster near anterior lateral CA1. The authors state, “Our results show that for associations between objects, between objects and 2D space, or between objects and 3D space, the hippocampus does not seem to favor one type of representation over another; it is not a story of exclusivity.” Hence, these results are important because they add nuance to hippocampal theories of cognition, showing that both scene construction and other relational processing are important. Unaccounted variability in anatomical damage within the hippocampus could mask selective deficits in one process versus another or produce discrepant patterns across studies (also see Mullally et al., 2012). Our patients’ MRI scans do not have the resolution to explore damage in the small subregions of the hippocampus noted in Dalton et al. (2018). More critical, the anatomical proximity (e.g., in anterior hippocampus) between scenes and relational processes observed in Dalton et al. suggests that one would require patients with very discrete lesions to elucidate these processes further through patient work.

In summary, our study, which was designed to test a hypothesis put forth in the literature to explain verbal memory deficits in patients with hippocampal damage, shows that the hippocampus plays a critical role in verbal episodic memory irrespective of the scene construction

demands placed on the to-be-remembered information. Accordingly, we conclude that verbal memory performance in amnesia is not a byproduct of a scene construction deficit and other possible mechanisms must be considered.

Credit author statement

Daniela J. Palombo – Conceptualization, Methodology, Formal analysis, Writing, Editing. Dominoe Jones – Project Administration, Formal analysis, Writing, Editing. Caroline Strang – Project Administration, Formal analysis, Editing. Mieke Verfaellie – Conceptualization, Methodology, Formal analysis, Writing, Editing, Funding acquisition.

Data availability

Data will be made available on request.

Acknowledgements

We dedicate our paper to Andrew Mayes, a pioneer in the study of amnesia who inspired decades of research. This research was supported by grant I01CX000925 and a Senior Research Career Scientist Award to M.V., both from the Clinical Science and Development Service, US Department of Veterans Affairs. The authors thank Alessandra Te and Oliver Bonkes for research assistance. The contents of this manuscript do not represent the view of the US Department of Veterans Affairs or the US Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2023.108543>.

- _____

References

- Barry, D.N., Maguire, E.A., 2019. Remote memory and the Hippocampus: a constructive critique. *Trends Cognit. Sci.* 23 (2), 128–142. <https://doi.org/10.1016/j.tics.2018.11.005>.
- Balota, D.A., Yap, M.J., Cortese, M.J., Hutchison, K.A., Kessler, B., Loftis, B., Neely, J.H., Nelson, D.L., Simpson, G.B., Treiman, R., 2007. The English Lexicon Project. *Behav. Res. Methods* 39 (3), 445–459. <https://doi.org/10.3758/BF03193014>.
- Bird, C.M., Shallice, T., Cipolotti, L., 2007. Fractionation of memory in medial temporal lobe amnesia. *Neuropsychologia* 45 (6), 1160–1171. <https://doi.org/10.1016/j.neuropsychologia.2006.10.011>.
- Bird, C.M., Capponi, C., King, J.A., Doeller, C.F., Burgess, N., 2010. Establishing the boundaries: the hippocampal contribution to imagining scenes. *J. Neurosci.* 30 (35), 11688–11695. <https://doi.org/10.1523/JNEUROSCI.0723-10.2010>.
- Bird, C.M., Vargha-Khadem, F., Burgess, N., 2008. Impaired memory for scenes but not faces in developmental hippocampal amnesia: a case study. *Neuropsychologia* 46 (4), 1050–1059. <https://doi.org/10.1016/j.neuropsychologia.2007.11.007>.
- Caplan, J.B., Madan, C.R., 2016. Word imageability enhances association-memory by increasing hippocampal engagement. *J. Cognit. Neurosci.* 28 (10), 1522–1538. https://doi.org/10.1162/jocn_a_00992.
- Cipolotti, L., Bird, C., Good, T., Macmanus, D., Rudge, P., Shallice, T., 2006. Recollection and familiarity in dense hippocampal amnesia: a case study. *Neuropsychologia* 44 (3), 489–506. <https://doi.org/10.1016/j.neuropsychologia.2005.05.014>.
- Clark, I.A., Kim, M., Maguire, E.A., 2018. Verbal paired associates and the hippocampus: the role of scenes. *J. Cognit. Neurosci.* 30 (12), 1821–1845. https://doi.org/10.1162/jocn_a_01315.
- Clark, I.A., Maguire, E.A., 2016. Remembering preservation in hippocampal amnesia. *Annu. Rev. Psychol.* 67 (1), 51–82. <https://doi.org/10.1146/annurev-psych-122414-033739>.
- Clark, I.A., Monk, A.M., Maguire, E.A., 2020. Characterizing strategy use during the performance of hippocampal-dependent tasks. *Front. Psychol.* 11, 2119. <https://doi.org/10.3389/fpsyg.2020.02119>.
- Cohen, N.J., Eichenbaum, H., 1993. *Memory, Amnesia, and the Hippocampal System*. MIT Press, Cambridge, MA.
- Dalton, M.A., Maguire, E.A., 2017. The pre/parasubiculum: a hippocampal hub for scene-based cognition? *Curr. Opin. Behav. Sci.* 17, 34–40. <https://doi.org/10.1016/j.cobeha.2017.06.001>.
- Dalton, M.A., Zeidman, P., McCormick, C., Maguire, E.A., 2018. Differentiable processing of objects, associations, and scenes within the hippocampus. *J. Neurosci.* 38 (38), 8146–8159. <https://doi.org/10.1523/jneurosci.0263-18.2018>.
- Ekstrom, A.D., Ranganath, C., 2017. Space, time, and episodic memory: the hippocampus is all over the cognitive map. *Hippocampus* 28 (9), 680–687. <https://doi.org/10.1002/hipo.22750>.
- Eichenbaum, H., Cohen, N.J., 2014. Can we reconcile the declarative memory and spatial navigation views on hippocampal function? *Neuron* 83 (4), 764–770. <https://doi.org/10.1016/j.neuron.2014.07.032>.
- Fletcher, P.C., Shallice, T., Frith, C.D., Frackowiak, R.S., Dolan, R.J., 1996. Brain activity during memory retrieval. The influence of imagery and semantic cueing. *Brain* 119 (Pt 5), 1587–1596. <https://doi.org/10.1093/brain/119.5.1587>.
- Fließbach, K., Weis, S., Klaver, P., Elger, C.E., Weber, B., 2006. The effect of word concreteness on recognition memory. *Neuroimage* 32 (3), 1413–1421. <https://doi.org/10.1016/j.neuroimage.2006.06.007>.
- Graham, K.S., Barense, M.D., Lee, A.C.H., 2010. Going beyond LTM in the MTL: a synthesis of neuropsychological and neuroimaging findings on the role of the medial temporal lobe in memory and perception. *Neuropsychologia* 48 (4), 831–853. <https://doi.org/10.1016/j.neuropsychologia.2010.01.001>.
- Graham, K.S., Scallan, 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. *J. Neurosci.* 26 (29), 7547–7554. <https://doi.org/10.1523/JNEUROSCI.1535-06.2006>.
- Hartley, T., Bird, C.M., Chan, D., Cipolotti, L., Husain, M., Vargha-Khadem, F., Burgess, N., 2007. The hippocampus is required for short-term topographical memory in humans. *Hippocampus* 17 (1), 34–48. <https://doi.org/10.1002/hipo.20240>.
- Hassabis, D., Kumaran, D., Vann, S.D., Maguire, E.A., 2007. Patients with hippocampal amnesia cannot imagine new experiences. *Proc. Natl. Acad. Sci. USA* 104 (5), 1726–1731. <https://doi.org/10.1073/pnas.0610561104>.
- Hassabis, D., Maguire, E.A., 2007. Deconstructing episodic memory with construction. *Trends Cognit. Sci.* 11 (7), 299–306. <https://doi.org/10.1016/j.tics.2007.05.001>.
- Hodgetts, C.J., Shine, J.P., Lawrence, A.D., Downing, P.E., Graham, K.S., 2016. Evidencing a place for the hippocampus within the core scene processing network. *Hum. Brain Mapp.* 37 (11), 3779–3794. <https://doi.org/10.1002/hbm.23275>.
- Hoscheidt, S.M., Nadel, L., Payne, J., Ryan, L., 2010. Hippocampal activation during retrieval of spatial context from episodic and semantic memory. *Behav. Brain Res.* 212 (2), 121–132. <https://doi.org/10.1016/j.bbr.2010.04.010>.
- Howard, M.W., Shankar, K.H., Aue, W.R., Criss, A.H., 2015. A distributed representation of internal time. *Psychol. Rev.* 122 (1), 24–53. <https://doi.org/10.1037/a0037840>.
- JASP Team, 2022. *JASP (Computer software)*, Version 0.16.3.
- Jessen, F., Heun, R., Erb, M., Granath, D.-O., Klose, U., Papasotiropoulos, A., Grodd, W., 2000. The concreteness effect: evidence for dual coding and context availability. *Brain Lang.* 74 (1), 103–112. <https://doi.org/10.1006/brln.2000.2340>.
- Jones-Gotman, M., 1979. Incidental learning of image-mediated or pronounced words after right temporal lobectomy. *Cortex* 15 (2), 187–197. [https://doi.org/10.1016/s0010-9452\(79\)80024-6](https://doi.org/10.1016/s0010-9452(79)80024-6).
- Jones-Gotman, M., Milner, B., 1978. Right temporal-lobe contribution to image-mediated verbal learning. *Neuropsychologia* 16 (1), 61–71. [https://doi.org/10.1016/0028-3932\(78\)90043-x](https://doi.org/10.1016/0028-3932(78)90043-x).
- Kan, I.P., Giovanello, K.S., Schnyer, D.M., Makris, N., Verfaellie, M., 2007. Role of the medial temporal lobes in relational memory: neuropsychological evidence from a cued recognition paradigm. *Neuropsychologia* 45 (11), 2589–2597. <https://doi.org/10.1016/j.neuropsychologia.2007.03.006>.
- Kim, S., Dede, A.J., Hopkins, R.O., Squire, L.R., 2015. Memory, scene construction, and the human hippocampus. *Proc. Natl. Acad. Sci. U. S. A* 112 (15), 4767–4772. <https://doi.org/10.1073/pnas.1503863112>.
- Klaver, P., Fell, J., Dietl, T., Schür, S., Schaller, C., Elger, C.E., Fernández, G., 2005. Word imageability affects the hippocampus in recognition memory. *Hippocampus* 15 (6), 704–712. <https://doi.org/10.1002/hipo.20081>.
- Konkel, A., Cohen, N.J., 2009. Relational memory and the hippocampus: representations and methods. *Front. Neurosci.* 3 (2), 166–174. <https://doi.org/10.3389/neuro.01.023.2009>.
- Konkel, A., Warren, D.E., Duff, M.C., Tranel, D.N., Cohen, N.J., 2008. Hippocampal amnesia impairs all manner of relational memory. *Front. Hum. Neurosci.* 2, 15. <https://doi.org/10.3389/neuro.09.015.2008>.
- Lynch, K., Keane, M.M., Verfaellie, M., 2020. The status of semantic memory in medial temporal lobe amnesia varies with demands on scene construction. *Cortex* 131, 114–122. <https://doi.org/10.1016/j.cortex.2020.07.005>.
- Maguire, E.A., Mullally, S.L., 2013. The hippocampus: a manifesto for change. *J. Exp. Psychol. Gen.* 142 (4), 1180–1189. <https://doi.org/10.1037/a0033650>.
- Maguire, E.A., Nannery, R., Spiers, H.J., 2006. Navigation around London by a taxi driver with bilateral hippocampal lesions. *Brain* 129 (Pt 11), 2894–2907. <https://doi.org/10.1093/brain/awl286>.
- Murray, E.A., Wise, S.P., Graham, K.S., 2018. Representational specializations of the hippocampus in phylogenetic perspective. *Neurosci. Lett.* 680, 4–12. <https://doi.org/10.1016/j.neulet.2017.04.065>.
- Mullally, S.L., Hassabis, D., Maguire, E.A., 2012. Scene construction in amnesia: an FMRI study. *J. Neurosci.* 32 (16), 5646–5653. <https://doi.org/10.1523/JNEUROSCI.5522-11.2012>.
- O'Keefe, J., Nadel, L., 1978. *The hippocampus as a Cognitive Map*. Clarendon Press, Oxford, UK.

- Paivio, A., Smythe, P.C., Yuille, J.C., 1968. Imagery versus meaningfulness of nouns in paired-associate learning. *Can. J. Psychol.* 22 (6), 427–441. <https://doi.org/10.1037/h0082782>.
- Palombo, D.J., Sheldon, S., Levine, B., 2018. Individual differences in autobiographical memory. *Trends Cognit. Sci.* 22 (7), 583–597. <https://doi.org/10.1016/j.tics.2018.04.007>.
- Palombo, D.J., Di Lascio, J.M., Howard, M.W., Verfaellie, M., 2019. Medial temporal lobe amnesia is associated with a deficit in recovering temporal context. *J. Cognit. Neurosci.* 31 (2), 236–248. https://doi.org/10.1162/jocn_a.01344.
- Peters, J., Daum, I., 2008. Differential effects of normal aging on recollection of concrete and abstract words. *Neuropsychology* 22 (2), 255–261. <https://doi.org/10.1037/0894-4105.22.2.255>.
- Polyn, S.M., Norman, K.A., Kahana, M.J., 2009. A context maintenance and retrieval model of organizational processes in free recall. *Psychol. Rev.* 116 (1), 129–156. <https://doi.org/10.1037/a0014420>.
- Roberts, B.M., Libby, L.A., Inhoff, M.C., Ranganath, C., 2018. Brain activity related to working memory for temporal order and object information. *Behav. Brain Res.* 354, 55–63. <https://doi.org/10.1016/j.bbr.2017.05.068>.
- Robin, J., Buchsbaum, B.R., Moscovitch, M., 2018. The primacy of spatial context in the neural representation of events. *J. Neurosci.* 38 (11), 2755–2765. <https://doi.org/10.1523/JNEUROSCI.1638-17.2018>.
- Rosenbaum, R., Shayna, 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 (12), 1619–1635. <https://doi.org/10.1016/j.neuropsychologia.2004.04.010>.
- 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. *Nat. Neurosci.* 3 (10), 1044–1048. <https://doi.org/10.1038/79867>.
- Ross, D.A., Sadil, P., Wilson, D.M., Cowell, R.A., 2018. Hippocampal engagement during recall depends on memory content, 1699 *Cerebr. Cortex* 29 (4), 1699. <https://doi.org/10.1093/cercor/bhy182>.
- Ryan, J.D., Althoff, R.R., Whitlow, S., Cohen, N.J., 2000. Amnesia is a deficit in relational memory. *Psychol. Sci.* 11 (6), 454–461. <https://doi.org/10.1111/1467-9280.00288>.
- Ryan, L., Lin, C.Y., Ketcham, K., Nadel, L., 2010. The role of medial temporal lobe in retrieving spatial and nonspatial relations from episodic and semantic memory. *Hippocampus* 20 (1), 11–18. <https://doi.org/10.1002/hipo.20607>.
- Schacter, D.L., Addis, D.R., 2007. The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Phil. Trans. Biol. Sci.* 362 (1481), 773–786. <https://doi.org/10.1098/rstb.2007.2087>.
- Scoville, W.B., Milner, B., 1957. Loss of recent memory after bilateral hippocampal lesions. *J. Neurol. Neurosurg. Psychiatr.* 20 (1), 11–21. <https://doi.org/10.1136/jnnp.20.1.11>.
- Shimamura, A.P., Squire, L.R., 1986. Memory and metamemory: a study of the feeling-of-knowing phenomenon in amnesic patients. *J. Exp. Psychol. Learn. Mem. Cognit.* 12 (3), 452–460. <https://doi.org/10.1037/0278-7393.12.3.452>.
- Taylor, K.J., Henson, R.N., Graham, K.S., 2007. Recognition memory for faces and scenes in amnesia: dissociable roles of medial temporal lobe structures. *Neuropsychologia* 45 (11), 2428–2438. <https://doi.org/10.1016/j.neuropsychologia.2007.04.004>.
- Zeidman, P., Lutti, A., Maguire, E.A., 2015. Investigating the functions of subregions within anterior hippocampus. *Cortex* 73, 240–256. <https://doi.org/10.1016/j.cortex.2015.09.002>.
- Zola-Morgan, S., Squire, L.R., Amaral, D.G., 1986. Human amnesia and the medial temporal region: enduring memory impairment following a bilateral lesion limited to field CA1 of the hippocampus. *J. Neurosci.* 6 (10), 2950–2967. <https://doi.org/10.1523/JNEUROSCI.06-10-02950>.

Further reading

- Allen, M., Poggiali, D., Whitaker, K., Marshall, T.R., van Langen, J., Kievit, R.A., 2021. Raincloud plots: a multi-platform tool for robust data visualization. *Well. Open Res.* 4, 63. <https://doi.org/10.12688/wellcomeopenres.15191.2>.