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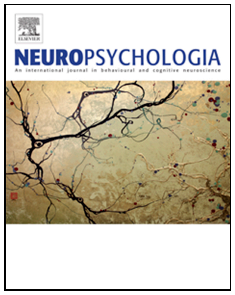

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The language of mental images: Characterizing hippocampal contributions to imageable word use during event construction

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Abstract

Accumulating evidence suggests that the hippocampus plays a critical role in the creative and flexible use of language at the sentence or discourse level. Yet it is currently unclear whether the hippocampus also supports language use at the level of single words. A recent study by Hilverman and colleagues (2017) found that amnesic patients with hippocampal damage use less imageable words when describing autobiographical episodes compared to healthy controls, but this deficit was attributed to patients' deficits in episodic memory rather than impairments in linguistic functions of the hippocampus per se. Yet, in addition to affecting word use by way of its role in memory, the hippocampus could also impact language use more directly. The current study aimed to test this hypothesis by investigating the status of imageable word use in amnesia during two different types of language production tasks. In Experiment 1, participants constructed narratives about events depicted in visually presented pictures (picture narratives). In Experiment 2, participants constructed verbal narratives about remembered events from the past or simulated events in the future (past/future narratives). Across all types of narratives, patients produced words that were rated as having similar levels of imageability compared to controls. Importantly, this was the case both in patients' picture narratives, which did not require generating details from episodic memory and were matched to those of controls with respect to narrative content, and in patients' narratives about past/future events, which required generating details from memory and which were reduced in narrative content compared to those of controls. These results distinguish between the quantity and quality of individual linguistic details produced in amnesia during narrative construction, and suggest that the use of imageable linguistic representations does not depend on intact episodic memory and can be supported by regions outside the hippocampus.

Key Words: medial temporal lobe, episodic memory, language production

1. Introduction

Accumulating evidence suggests that in addition to its pivotal role in episodic memory, the hippocampus also supports cognitive functions outside the domain of long-term memory, such as visual perception, attention, and short-term memory (Aly & Turk-Browne, 2018; Lee et al., 2005; Moscovitch, Cabeza, Winocur, & Nadel, 2016; Olsen, Moses, Riggs, & Ryan, 2012; Shohamy & Turk-Browne, 2013; Turk-Browne, 2019). Recently, there has been growing interest in potential linguistic functions of the hippocampus (Corballis, 2019; Duff & Brown-Schmidt, 2012; Piai et al., 2016). Much of the evidence for hippocampal involvement in language has come from the study of language production in amnesic patients with hippocampal damage. Although linguistic functions are largely intact in these patients (Kensinger, Ullman, & Corkin, 2001; Milner, 1968; Skotko, Andrews, & Einstein, 2005; but see MacKay, Burke, & Stewart, 1998), hippocampal damage has been linked to qualitative changes in language production, particularly when constructing detailed narratives that unfold over time (Duff, Hengst, Tranel, & Cohen, 2009; Hilverman, Cook, & Duff, 2017; MacKay, Burke, & Stewart, 1998; Race, Keane, & Verfaellie, 2015). For example, when describing personally experienced past events or imagined future events, amnesic patients with hippocampal damage produce narratives that lack temporal organization and are reduced in narrative cohesion and coherence (Caspari & Parkinson, 2000; Kurczek & Duff, 2011; MacKay et al., 1998; Race et al., 2015; Heyworth & Squire, 2019). Such results suggest that in addition to its canonical role in episodic memory, the hippocampus plays a critical role in online language use, particularly when integrating and maintaining relations between linguistic elements at the sentence or discourse level (see also Kurczek, Brown-Schmidt, & Duff, 2013; Duff & Brown-Schmidt, 2012; MacKay, James, Hadley, & Fogler, 2011; Olsen et al., 2012). Additional evidence for hippocampal contributions to online language use and processing comes from recent electrophysiological and neuroimaging studies which have demonstrated hippocampal activity during sentence processing as language unfolds (Piai et al., 2016; Jafarpour et al, 2017; Bonhange et al., 2015).

Whereas existing evidence suggests that the hippocampus supports the constructive and flexible use of language at the level of sentences and extended discourse, it is currently unclear whether the hippocampus also supports language use at the level of single words. Several studies have shown that damage to the hippocampus or medial temporal lobes (MTL) can affect word use when describing autobiographical episodes, suggesting that this may be the case. For example, amnesic patients with MTL lesions use higher-frequency (i.e., more common) words, fewer nouns, and fewer instances of the historical present (present tense words that refer to a past action) compared to healthy controls (Heyworth & Squire, 2019; Hilverman et al., 2017; Park, St-Laurent, McAndrews, & Moscovitch, 2011). However, these differences in word use have been interpreted not as reflecting a direct linguistic function of the hippocampus, but rather as the result of impoverished episodic memory. That is, when autobiographical episodes are less vividly reexperienced, as is the case following MTL damage, their verbal description may be altered as a result.

A similar interpretation was offered for the pattern of deficits observed in a recent study by Hilverman and colleagues (2017). In that study, amnesic patients with damage to the hippocampus used words that were less imageable compared to those used by controls when constructing verbal narratives about events occurring in the lived past, imagined past, imagined present, or imagined future. Word imageability is a measure of the degree to which a word evokes a mental image or generates an internal visual representation (Paivio, Yuille, & Madigan, 1968). For example, the word "eagle" is rated higher in imageability than the word "trust." The finding that patients used less imageable words compared to controls was interpreted as reflecting patients' long-term memory deficits, which prevented them from constructing imageable mental representations of the past, present, or future: "When declarative (episodic) representations are impoverished, or less imageable, the words used to convey those mental representations in language are also less imageable." Indeed, healthy individuals have been shown to use less imageable words when describing more distant memories that have faded over time (e.g., when describing events from the remote versus recent past) (Heyworth & Squire, 2019), consistent with the notion that the nature of the mental representation being described affects the words used to describe it (Hilverman et al., 2017).

Yet in addition to affecting word use by way of its role in episodic memory, the hippocampus could also impact language use more directly. For example, prior studies have suggested that the hippocampus may contribute to the processing, representation, or retrieval of individual words given that activity in the hippocampus increases during naming tasks that place low demands on episodic memory, such as picture naming (e.g., Hamamé et al., 2014; Bonelli, Powell, Thompson, Yogarajah, et al., 2011; but see Bauer, Swanson, Sabsevitz, Gross, et al. 2017). With respect to word imageability, recent neuroimaging studies have found that stimulus imageability modulates activity in the hippocampus and MTL cortex both in memory tasks (e.g., Caplan & Madan, 2016; Klaver et al., 2005) and in non-memory tasks such as word association and semantic similarity (Bonner, Price, Peelle, & Grossman, 2016; Sabsevitz, Medler, Seidenberg, & Binder, 2005; Wise et al., 2000). Together, such findings raise the possibility that the hippocampus may play a more direct role in word use, and the use of imageable words in particular, distinct from its canonical role in episodic memory.

The current study aimed to further test this hypothesis by investigating the status of imageable word use in amnesic patients with hippocampal damage. In Experiment 1, we tested whether amnesic patients produce less imageable words than healthy controls in two types of picture description tasks. Picture description provides a constrained method of eliciting verbal narratives and has been widely used to assess the language abilities of clinical populations (Bird, Lambon Ralph, Patterson, & Hodges, 2000). In these tasks, participants are shown a picture of a scene and may be instructed to describe what they see in the picture (picture description) or to tell a *story* about the events depicted in the picture (picture story). Importantly, these picture narratives place fewer demands on episodic memory than autobiographical narrative tasks (Race et al., 2011; Hilverman et al., 2017). Although participants can potentially draw upon schematic knowledge when constructing these narratives (Keven et al., 2018), particularly in the picture story condition, which allows more room for extrapolation beyond the events depicted in the picture, in both cases narrative content is provided by the picture and does not need to be generated from episodic memory. Indeed, prior work has demonstrated that amnesic patients produce a similar amount of narrative content in these picture narrative tasks compared to controls, indicating that performance does not depend on episodic memory (Race et al., 2011; Race, Keane, & Verfaellie, 2013; Keven et al., 2018). An outstanding question is whether the words in patients' picture narratives are as imageable as those in the narratives of controls. If the hippocampus plays a direct role in imageable word use that is distinct from its role in episodic memory, amnesic patients should use less imageable words compared to controls. To foreshadow our results, we found that patients and controls used similarly imageable words in their picture narratives, suggesting that the hippocampus does not play a direct role in imageable word use.

Whereas the results of Experiment 1 are consistent with the proposal that the contribution of the hippocampus to imageable word use is mediated by its established role in episodic memory (Hilverman et al., 2017), a recently study by Heyworth and Squire (2019) raises questions about the relationship between the hippocampus, episodic memory, and imageable word use. In that study, the authors found that amnesic patients with hippocampal damage could produce imageable words as well as controls in a narrative task that clearly draws upon episodic memory. Specifically, amnesic patients with hippocampal damage and healthy controls were taken on a 25-min guided walk and were then instructed to recall the events of the walk. Patients' recollections of the guided walk were impoverished and lacking in detail, consistent with their severe deficits in episodic memory. However, surprisingly, amnesic patients did not use less imageable words in their narratives compared to controls. This result stands in contrast to the imageability deficits observed in amnesia in the study by Hilverman and colleagues (2017), and it is currently unclear what factors contribute to the different patterns of results observed across studies. Among others, differences in the patient groups (and their lesion profiles) or in the nature of the task demands are plausible candidates. More broadly, given that only two prior studies have assessed the imageability of the words used by amnesic patients to describe autobiographical narratives, more data is needed to determine the status of imageable word use following hippocampal damage. Therefore, in Experiment 2 we conducted a re-analysis of previously acquired autobiographical narratives about the past and future collected from amnesic patients and healthy controls. As was the case in the study by Hilverman and colleagues (2017), these narratives require retrieving and using details stored in long-term memory to construct an unfolding narrative, and have been shown to be less detailed in amnesic patients with damage to the hippocampus (Race et al., 2011). If the hippocampus contributes to the production of imageable words through its role in episodic memory, deficits in imageable word use in amnesia should occur in these future/past narratives.

Experiment 1: Picture Narratives

2. Materials and Methods

2.1 Participants

Nine amnesic patients with MTL lesions participated in the study. All of the amnesic patients participated in a prior study investigating discourse cohesion and coherence in narratives about novel future events, experienced past events, and events in pictures (Race et al., 2015). In addition, eight of the amnesic patients participated in a prior study investigating the nature of the content of these narratives (Race et al., 2011). Neuropsychological profiles for the patients are described in Table 1 and indicate severe impairments isolated to the domain of memory with profound deficits in new learning. Volumetric data for the hippocampus and MTL cortices were available for five patients. Two of the anoxic patients (P05 and P09) had damage limited to the hippocampus, and two of the encephalitic patients (P01 and P02) and one of the anoxic patients (P04) had damage to the hippocampus and surrounding parahippocampal gyrus. No common volume reductions were found outside the hippocampus. MRI could not be obtained for the remaining patients because of medical contraindications. For the encephalitic patient P06, a computerized tomography (CT) scan was available and visual inspection indicated extensive hippocampal and parahippocampal gyrus damage. For the remaining patients, MTL pathology can be inferred on the basis of etiology and neuropsychological profile.

Twelve healthy controls also participated, all of whom had participated in the prior studies by Race et al. (2011; 2015). The control subjects were matched to the patient group in terms of mean age (60 ± 12.2 years), education (14 ± 2.0 years), and verbal IQ (105 ± 15.7). As reported by Race et al. (2011, 2013), quantitative assessment revealed that the patients' descriptions of the future and past contained fewer episodic details than those of controls, whereas their picture descriptions contained an equivalent number of episodic details compared to those of controls. This pattern of impairment was also present in the additional amnesic patient included in the present study (P09), who provided fewer episodic details than controls in his future and past narratives (z scores < -2) but did not provide fewer episodic details in his picture narratives (z scores > .9). All participants were paid for their participation and provided informed consent in accordance with the procedures of the Institutional Review Boards at Boston University and the VA Boston Healthcare System.

[Insert Table 1 Here]

2.2 Stimuli

This study is a reanalysis of the picture narrative data reported by Race et al. (2011; 2013). Participants were shown detailed drawings of scenes, one at a time, that depicted characters engaged in various activities (e.g., a picnic at a park). In the “picture description” condition, participants were instructed to describe what they saw in the picture in as much detail as possible without creating a story about the picture (Race et al., 2013). In the “picture story” condition, participants were instructed to imagine that the picture was a scene taken from a movie and to tell a story about what was going on in the scene (Race et al., 2011). Five narratives in each condition were audiotaped and transcribed for analysis.

2.3 Scoring

Narratives were scored following the procedures used by Hilverman et al. (2017). Words in each narrative were first coded as either a function word or a content word. Content words were defined as adjectives, adverbs, nouns, and verbs. Function words included pronouns (i.e. she, me, it, what, etc.), auxiliary verbs (i.e. do, have, been, etc.), articles (i.e. the, an, etc.), particles (i.e. well, um, etc.), and conjunctions (i.e. and, but, if, etc.) The MRC Psycholinguistic database was used to score each unique content word for verbal frequency and imageability. More information on these measures can be found on the MRC Psycholinguistic database website (http://websites.psychology.uwa.edu/school/MRCDatabase/ uwa_mrc.htm). Contractions were manually changed to non-contracted words before scoring. Words not included in the MRC database were not scored. The percentage of unique content words scored in each type of narrative did not differ for patients (M = 50%) and controls (M = 51%) ($t(19) = 2.19$, $p = .31$).

2.4 Bayesian Analyses

Our primary data analysis followed the frequentist tradition with an alpha level set at $p <$ .05. For results that did not reach statistical significance, Bayesian analyses were also performed using JASP (JASP Team, 2018) using default priors to examine the relative support for the null and the alternative hypotheses. Reported Bayes Factors (B_{10}) represent the evidence for alternative model (H1) relative to the null model (H0).

3. Results

3.1 Word Count

Healthy control participants produced an average of 205 total words (*SD* = 95) per narrative and amnesic patients produced an average of 158 total words (*SD* = 90) per narrative. Total word count was entered into a two-way mixed factorial ANOVA with factors of group (control, patient) and picture narrative condition (picture description, picture story). There was no main effect of group ($F(1,19) = 1.46$, $p = .24$, $\eta_p^2 = .07$, $BF_{10} = .82$), indicating that the number of words produced by patients and controls in the picture narrative tasks did not significantly differ. There was also no main effect of picture narrative condition ($F(1,19) = 3.10$, $p = .09$, $\eta_p^2 = .14$, $BF_{10} = 1.11$) nor group x condition interaction ($F(1,19) = .43$, $p = .52$, $\eta_p^2 = .02$, $BF_{10} = .50$). We next analyzed whether there was any difference in the number of unique content words used by each group of participants. Healthy control participants produced an average of 69 unique content words (*SD* = 24) and amnesic patients produced an average of 56 unique content words (*SD* = 28) per narrative. A two-way mixed factorial ANOVA with factors of group (control, patient) and narrative condition (picture description, picture story) revealed that there was no main effect of group ($F(1,19) = 1.39$, $p = .26$, $\eta_p^2 = .07$, $BF_{10} = .92$). There was also no main effect of picture narrative condition ($F(1,19) = 1.71$, $p = .21$, $\eta_p^2 = .08$, $BF_{10} = .60$) nor group x condition interaction ($F(1,19) = .03$, $p = .87$, $\eta_p^2 = .002$, $BF_{10} = .40$).

3.2 Verbal Frequency

The unique content words produced by healthy controls and amnesic patients were similar in terms of mean verbal frequency (controls: *M* = 217, *SD* = 42; patients: *M* = 231, *SD* = 51). When verbal frequency ratings were entered into a two-way mixed factorial ANOVA with factors of group (control, patient) and picture narrative condition (picture description, picture story), there was no main effect of group ($F(1,19) = .96$, $p = .34$, $\eta_p^2 = .05$, $BF_{10} = .50$). There was also no main effect of condition ($F(1,19) = 3.66$, $p = .07$, $\eta_p^2 = .16$; $BF_{10} = 2.14$) nor group x condition interaction ($F(1,19) = .008$, $p = .93$, $\eta_p^2 < .001$; $BF_{10} = .39$).

3.3 Imageability

Our primary analysis of interest concerned the imageability ratings of the unique words produced by amnesic patients and healthy controls (**Figure 1A**). The average imageability ratings were remarkably similar across groups (controls: M = 450, SD = 35; patients: M = 452, SD = 23). Word imageability ratings were entered into a two-way mixed factorial ANOVA with factors of group (control, patient) and narrative condition (picture description, picture story). A main effect of condition ($F(1,19) = 19.79$, $p < .001$, $\eta_p^2 = .51$) reflected that words produced in participants' picture description narratives were more imageable than words produced in participants' picture story narratives. However, there was no main effect of group ($F(1,19) = .03$, $p = .86$, $\eta_p^2 = .002$; $BF_{10} = .38$) nor group x time period interaction ($F(1,19) = 1.85$, $p = .19$, $\eta_p^2 = .09$; $BF_{10} = .86$), indicating that the imageability of the words used in patients' and controls' picture narratives did not significantly differ. Data from the picture description and picture story narratives were also analyzed using a one-way ANCOVA with word count and verbal frequency as covariates. When adjusting for word count and verbal frequency, there was still no significant main effect of group for either picture description narratives ($F(1,17) = .31$, $p = .58$, $\eta_p^2 = .02$, ; $BF_{10} = .43$) nor picture story narratives ($F(1,17) = 3.96$, $p = .06$, $\eta_p^2 = .19$, $BF_{10} = .57$). In fact, post-hoc analysis of the adjusted marginal means revealed that patients used words that had numerically higher imageability ratings (M = 444) in their picture story narratives compared to controls (M = 430). The finding that patients and controls use similarly imageable words in their picture narratives was confirmed on an individual basis when looking at patients' z-scores: None of the individual patients demonstrated significantly impaired performance compared to controls as defined by a z-score cut-off of -1.96 (z score range: -1.49 to 1.52).

[Insert Figure 1 Here]

3.4 Relationship to Episodic Memory

We next explored whether the imageability ratings of the words produced in patients' picture narratives were related to the extent of patients' deficit in episodic memory as measured by neuropsychological assessment. For picture story narratives, there was no correlation between patients' imageability ratings and their scores on the Visual Delay ($r = .03$, $p = .94$) or General Memory ($r = -.33$, $p = .39$) subscales of the Wechsler Memory Scale, III. For picture description narratives, there was also no correlation between patients' imageability ratings and their scores on the Visual Delay or General Memory subscales of the Wechsler Memory Scale, III ($r = .58$, $p = .10$; $r = .50$, $p = .17$, respectively).

3.5 Distribution of Imageability Scores

To examine whether the distribution of imageable words used by patients and controls differed, we performed an additional analysis of the number of words used by each group in each quintile of imageability ratings (**Supplementary Table 1**). The range of imageability ratings was first calculated across healthy controls, separately for picture description narratives and for picture story narratives, in order to define five quintile bins for each type of picture narrative. The number of unique words in each quintile bin was then counted in each participant and the distributions were compared in patients and controls using a Chi-Square test. For picture description narratives, the distribution of words across imageability bins did not differ between patients and controls (X^2 (2, N = 21) = .12, p = .99). For picture story narratives, the distribution of words across imageability bins also did not differ between patients and controls (X^2 (2, N = 21) = .81, p = .94).

4. Interim Discussion

The results from Experiment 1 demonstrate that when constructing two different types of narratives about visually presented pictures, patients with amnesia use words that are similar in imageability to those used by controls. Importantly, these picture narratives did not require retrieval of narrative content from episodic memory and were matched in terms of narrative content across patients and controls. These findings are consistent with the proposal that previously observed reductions in imageable word use in amnesia reflect hippocampal contributions to episodic memory rather than language production per se (Hilverman et al., 2017). However, recent evidence suggests that amnesic patients with hippocampal damage can use imageable words when describing autobiographical episodes, even when memory for these episodes is impoverished and lacking in detail (Heyworth & Squire, 2019). Thus, Experiment 2 aimed to further test the relationship between the hippocampus, long-term memory, and imageable word use by investigating patients' word use when constructing autobiographical narratives that draw upon episodic memory and have been shown to be impoverished in amnesia (past/future narratives).

Experiment 2: Future and Past Narratives

5. Materials and Methods

5.1 Participants

The same participants were tested in Experiments 1 and 2.

5.2 Stimuli

This study is a reanalysis of past/future narrative data reported by Race et al. (2011; 2015). Narratives about the past and the future were generated by having participants either recall specific personal events about the past (e.g., graduation ceremony) or imagine specific personal events about the future (e.g., winning the lottery). Participants were given three minutes to describe the event in as much detail as possible, and were instructed to describe where and when the event is taking place, who is there, how they feel, and what they are thinking. Within the allotted three minutes, participants continued with their descriptions without interference from the examiner until they came to a natural ending point. Narratives were audiotaped and transcribed for analysis. In the current study, two narratives about the future and two narratives about the past were selected from the larger sample for analysis (mirroring the procedures used by Race et al., 2015).

5.3 Scoring

Narratives were scored following the same procedures used in Experiment 1. The percentage of unique content words scored in each type of narrative did not differ for patients and controls in narratives about the past (*M* = 68% and 67%, respectively) or narratives about the future (*M* = 64% and 66%, respectively) (*t*s(19) < .44, *p*s > .66).

5.4 Bayesian Analyses

Our primary data analysis followed the frequentist tradition with an alpha level set at $p < .05$. For results that did not reach statistical significance, Bayesian analyses were also performed using JASP (JASP Team, 2018) using default priors to examine the relative support for the null and the alternative hypotheses. Reported Bayes Factors (B_{10}) represent the evidence for alternative model (H1) relative to the null model (H0).

6. Results

6.1 Word Count

Healthy control participants produced an average of 125 words (*SD* = 50) per narrative and amnesic patients produced an average of 78 words (*SD* = 47) per narrative. Total word count was entered into a two-way mixed factorial ANOVA with factors of group (control, patient) and time period (past, future). There was a main effect of group ($F(1,19) = 6.09$, $p = .02$, $\eta_p^2 = .24$), indicating that patients produced overall fewer words than controls, but no main effect of time period (F(1,19) = .009, p = .93, η_p^2 = .001, BF_{10} = .29) nor group x time period interaction (F(1,19) = .05, p = .83, η_p^2 = .002, BF_{10} = .34). We next analyzed whether there was any difference in the number of unique content words used by each participant group, again using a two-way mixed factorial ANOVA with factors of group (control, patient) and time period (past, future). There was a main effect of group (F(1,19) = 6.63, p = .02, η_p^2 = .26), reflecting that patients produced fewer unique content words than controls, but no main effect of time period (F(1,19) = .20, p = .66, η_p^2 = .009, BF_{10} = .33) nor group x time period interaction (F(1,19) = .02, p = .88, η_p^2 = .001, BF_{10} = .39). Together, these results converge with the prior finding that amnesic patients produce narratives about the past and future that contain fewer episodic details compared to those of controls (Race et al., 2011).

6.2 Verbal Frequency

The mean verbal frequency of the unique content words produced by healthy controls and amnesic patients in their future/past narratives were similar (controls: M = 291, SD = 41; patients: M = 275, SD = 78). When verbal frequency ratings were entered into a two-way mixed factorial ANOVA with factors of group (control, patient) and picture narrative condition (future, past), there was no main effect of group (F(1,19) = .82, p = .38, η_p^2 = .04, BF_{10} = .45). There was also no main effect of condition (F(1,19) = .47, p = .50, η_p^2 = .02, BF_{10} = .34) nor group x condition interaction (F(1,19) = 2.08, p = .17, η_p^2 = .10, BF_{10} = 1.10).

6.3 Imageability

The average imageability rating of content words produced in narratives about the past and future was very similar in healthy controls (M = 392; SD = 22) and amnesic patients (M = 400; SD = 24) (**Figure 1B**). When data were entered into a two-way mixed factorial ANOVA with factors of group (control, patient) and time period (past, future), there was a main effect of time period (F(1,19) = 9.33, p = .007, η_p^2 = .33), indicating that words produced in past narratives were more imageable than words produced in future narratives, similar to the findings reported by Hilverman and colleagues (2017). However, there was no main effect of group (F(1,19) = 1.10, p = .31, η_p^2 = .06, BF_{10} = .52) nor group x time period interaction (F(1,19) = .12, p = .73, η_p^2 = .006, BF_{10} = .40), indicating that the words produced in patients' and controls' narratives were similarly imageable. Data from the past and future narratives were also analyzed using a one-way ANCOVA with word count, verbal frequency, and proportion of episodic details as covariates. There was no main effect of group when adjusting for word count, verbal frequency, and proportion of episodic features for narratives about past events ($F(1,16) = 1.47$, $p = .24$, $\eta_p^2 = .08$, $BF_{10} = .57$) or narratives about future events ($F(1,16) = 3.53$, $p = .08$, $\eta_p^2 = .18$, $BF_{10} = .46$). For future events, the trend towards a difference in adjusted imageability ratings between patient and controls reflected numerically *greater* imageability ratings in patients ($M = 398$) compared to controls ($M = 379$). Covariate-adjusted imageability ratings (studentized residuals) were also greater for past compared to future narratives ($F(1,19) = 9.33$, $p < .01$, $\eta_p^2 = .33$). The finding that patients and controls use similarly imageable words in their narratives about the past and future was confirmed on an individual basis when looking at patients' z-scores: None of the individual patients demonstrated significantly impaired performance compared to controls as defined by a z-score cut-off of -1.96 (z score range: -1.45 to +2.30).

6.4 Relationship to Episodic Memory

We next explored whether the imageability ratings of the words produced in patients' narratives about the past or future were related to the extent of patients' deficit in episodic memory as measured by neuropsychological assessment. No correlation was found between imageability ratings in patients' past narratives and their scores on the Visual Delay subscale ($r = -.03$, $p = .94$) or General Memory subscale ($r = -.05$, $p = .88$) of the Wechsler Memory Scale, III. Similarly, no correlation was found between imageability ratings in patients' future narratives and their scores on the Visual Delay subscale ($r = -.25$, $p = .51$) or General Memory subscale ($r = -.17$, $p = .67$) of the Wechsler Memory Scale, III. Furthermore, there was also no correlation between imageability ratings in patients' past or future narratives and the proportion of episodic details produced in these narratives (past: $r = .17$, $p = .47$; future: $r = .42$, $p = .06$).

6.5 Distribution of Imageability Scores

To examine whether the distribution of imageable words used by patients and controls differed, we performed an additional analysis of the number of words used by each group in each quintile of imageability ratings (**Supplementary Table 1**). The range of imageability ratings was first calculated across healthy control participants, separately for past and for future narratives, in order to define five quintile bins for each type of narrative. The number of unique words in each quintile bin was then counted in each participant and the distributions were compared in patients and controls using a Chi-Square test. For past narratives, the distribution of words across imageability bins did not differ between patients and controls (X^2 (2, $N = 21$) = .19, $p = .99$). For future narratives, the distribution of words across imageability bins also did not differ between patients and controls (X^2 (2, $N = 21$) = .30, $p = .99$).

7. General Discussion

The current study investigated whether the hippocampus plays a critical role in imageable word use during narrative construction that can be distinguished from its canonical role in episodic memory. In four different types of verbal narratives, amnesic patients with hippocampal lesions were able to generate imageable words as well as controls. This was the case both for (1) picture narratives, which do not require mentally generating details from episodic memory and are matched across groups in terms of narrative content, and (2) narratives about the past and future, which depend on access to episodic memory representations, and for which patients generate fewer details than controls. These results distinguish between the quantity and quality of individual linguistic details produced in amnesia during narrative construction, and suggest that the use of imageable linguistic representations does not depend on intact episodic memory and can be supported by regions outside the hippocampus.

Although not included in traditional models of language, accumulating evidence suggests that the hippocampus contributes to the online use and processing of language, especially at the discourse level when linguistic elements must be flexibly integrated and maintained (Duff & Brown-Schmidt, 2012; Duff, Gupta, Hengst, Tranel, & Cohen, 2011; Kurczek, Brown-Schmidt, & Duff, 2013; Piai et al., 2016; Race et al., 2015). The contributions of the hippocampus to language use and processing have been attributed to its role in relational binding and the online integration of mnemonic and linguistic representations. However, a recent observation that amnesic patients with hippocampal damage produce less imageable words during narrative construction suggests that functions supported by the hippocampus also contribute to qualitative aspects of language use at the single word level (Hilverman et al., 2017). Importantly, the contribution of hippocampus to language use was proposed to reflect its established role in episodic memory, given that patients' use of less imageable words occurred in the context of autobiographical narrative tasks that drew upon episodic memory. The current study investigated whether the hippocampus also supports imageable word use more directly, in addition to influencing word use by way of its role in episodic memory. This question was motivated by recent neuroimaging studies which have observed hippocampal activity during naming tasks that do not rely on episodic memory (e.g, picture naming; Hamamé et al., 2014; Bonelli, Powell, Thompson, Yogarajah, et al., 2011) and by observations that stimulus imageability modulates activity in the hippocampus and MTL cortex in non-memory tasks (Bonner, Price, Peelle, & Grossman, 2016; Sabsevitz, Medler, Seidenberg, & Binder, 2005; Wise et al., 2000). In addition, prior work in amnesia could not distinguish between these possibilities given that deficits in imageable word use in amnesia always occurred in the context of concurrent deficits in narrative content. The observation in Experiment 1 that amnesic patients and controls produce similarly imageable words in two different picture description tasks that do not require retrieval from episodic memory reveals that the hippocampus is not always critical for the access or use of imageable representations at the linguistic level.

Experiment 2 was conducted to further examine whether the hippocampus plays a critical role in imageable word use in the context of narrative tasks that require retrieving details from episodic memory. Hilverman and colleagues (2017) previously proposed that the use of less imageable words in amnesia reflects patients' impoverished long-term memory representations. However, a recent study by Heyworth and Squire (2019) found that imageable word use was intact in amnesia even when verbal narratives draw heavily upon episodic memory. The findings of Experiment 2 provide further evidence that hippocampal contributions to episodic memory can be dissociated from potential contributions to imageable word use: Despite their severe deficits in episodic memory and the fact that they produced fewer details in their narratives about the past and future, amnesic patients produced individual narrative details that were as imageable as those generated by controls. In addition, no relationship was observed between the imageability of the words used in patients' narratives and the extent of their episodic memory deficits as measured by neuropsychological assessment. The dissociation between the quantity and quality of the individual details produced in patients' narratives, like that observed by Heyworth and Squire (2019), suggests that the level of detail comprising one's simulations of the past and future does not always affect the language used to describe these simulations. This observation is particularly interesting given that patients' verbal narratives about constructed events are typically rated as being qualitatively inferior (e.g., less vivid) compared to those constructed by controls (e.g., Hassabis et al., 2007; Kurczek et al., 2015). This raises the intriguing possibility that qualitative ratings of event narratives may be more closely related to overall features of the narrative, such as the amount of narrative detail or discourse-level features of continuity and contextual organization, rather than the quality of the individual words used to convey the narrative. Indeed, in prior work we demonstrated that amnesic patients produce narratives that are rated lower in measures of narrative coherence and cohesion (Race et al., 2015), both in the context of narratives that draw upon episodic memory (future/past narratives) and in the context of narratives that do not require retrieval from episodic memory (picture narratives). More broadly, the results of Experiment 2 converge with the prior results by Squire and Heyworth (2019) to suggest that the hippocampus does not always contribute to imageable word use in narrative tasks that draw upon episodic memory.

Why, then, might hippocampal lesions impair imageable word use in some contexts but not in others? Methodological differences between the present study, the study by Heyworth and

Squire (2019), and the study by Hilverman and colleagues (2017) may provide some insight into this question. In the Hilverman study, participants provided a one- to two-minute overview of an event and then constructed a narrative about the setting and experience of a specific moment within that event. Importantly, imageability ratings were only collected for words produced during the latter narrative when participants described a snapshot of time within the larger event. In contrast, participants in the present study and the study by Heyworth and Squire (2019) were instructed to construct narratives about sequences of events that unfolded more dynamically over time. This difference in the spatiotemporal context of the narrative (i.e., static vs. dynamic) likely influenced the degree to which participants used spatial imagery or spatial context during event construction and could have influenced the nature or phenomenology of retrieved representations or the constructed events more broadly. For example, it is known that the spatial features of retrieval cues can influence the vividness of remembered or imagined scenarios (Robin & Moscovitch, 2014, Hebscher, Levine, & Gilboa, 2018; Robin, Wynn, & Moscovitch, 2016; Sheldon & Chu, 2017) and that phenomenological aspects of memory retrieval are also influenced by the degree to which the layout of a scene is instantiated in memory (Rubin, Deffler, & Umanath, 2019). A recent study by Sheldon and colleagues (2019) directly compared the effects of emphasizing spatial versus action-based contexts prior to generating past and future autobiographical events, and found that emphasizing spatial context led to the generation of a greater proportion of perception-based details (e.g., sensory features of objects or spatial contextual elements) compared to emphasizing action-based details. Further, spatiotemporally specific cues might place higher demands on the integration of perceptual details, which has been proposed to influence the recruitment of the hippocampus during mental construction (Sheldon & Levine, 2016). Describing the details of a specific spatiotemporal event might also encourage more precise scene-based imagery, which has been associated with hippocampal function during memory and mental simulation (Hassabis & Maguire, 2007, St-Laurent, Moscovitch, Jadd, & McAndrews, 2014; Yonelinas, 2013, Cowell, Barense, & Sadil, 2019; Sheldon & Levine, 2016, Bird, Bisby, & Burgess, 2012, but see Kim et al., 2013). Though speculative, this proposal aligns with theories that emphasize spatiotemporal coding as a primary feature of hippocampal representation and coding (e.g., Byrne, Becker, & Burgess, 2007; Ekstrom & Ranganath, 2018; Ekstrom & Yonelinas, 2020; Hasselmo, Hinman, Dannenberg, & Stern, 2017; Turk-Browne, 2019; Robin, Buchsbaum, and Moscovitch, 2018). Indeed, increased activity in the hippocampus has been observed when remembering or imagining more spatiotemporally specific events (Addis, Cheng, Roberts, & Schacter, 2011; Palombo, Hayes, Peterson, Keane, & Verfaellie, 2018) and hippocampal activation has been shown to increase parametrically with the spatial specificity of an imagined scene (Bird, Capponi, King, Doeller, & Burgess, 2010). Future research should more directly test whether hippocampal contributions to the retrieval of imageable mnemonic representations during discourse depends on the spatiotemporal specificity of the narrative cues by experimentally manipulating this variable (i.e., directly comparing imageable word use in static and dynamic narratives within the same participants).

The presence of imageability impairments in amnesia may also depend on the extent and location of patients' lesions. Although the extent of patients' MTL lesions (e.g., lesion volumetrics) was not reported in the study by Hilverman and colleagues (2017), patients in that study were described as having "extensive bilateral medial temporal lobe damage affecting the hippocampus, amygdala, and surrounding cortices." Thus, it is possible that patients' use of less imageable words in that study reflects the presence of more extensive MTL lesions and neural damage in regions outside the hippocampus compared to the patients tested in the present study and the prior study by Heyworth and Squire (2019). In addition, recent theoretical models of hippocampal function have emphasized the functional heterogeneity of the hippocampus itself, for example along the anterior-posterior axis (Dalton, Zeidman, McCormick, & Maguire, 2018; Nadel, Hoscheidt, & Ryan, 2013; Poppenk, Evensmoen, Moscovitch, & Nadel, 2013; Strange, Witter, Lein, & Moser, 2014; Zeidman & Maguire, 2016; Sheldon, Fenerci, & Gurguryan, 2019; Sheldon & Levine, 2016; Poppenk et al., 2013; Dalton et al., 2018). Hippocampal lesions that differ across studies with respect to their anterior-posterior extent might therefore differentially affect the representation or access to more imageable information in memory. Future studies using higher-resolution structural or functional mapping could investigate whether specific regions along the anterior-posterior axis of the hippocampus are particularly important for the retrieval of imageable representations during event construction.

Finally, future research should also explore the degree to which the presence of deficits in imageable word use in amnesia depends on more mundane inter-experimental differences that might have differed across the prior study by Hilverman and colleagues (2017), which observed deficits in imageable word use, and the two studies that did not observe deficits in imageable word use (Heyworth & Squire, 2019 and the present study). For example, characteristics of the samples, the time period of the event described, and the manner in which events were probed could have influenced the pattern of results across studies. Future research that more carefully controls these variables will be important to shed light on the key factors that influence whether or not hippocampal lesions affect imageable word use.

In conclusion, the present neuropsychological results reveal that the hippocampus does not play an obligatory role in the use of imageable words during narrative construction, and that imageable word use can be intact following hippocampal lesions even in the face of severe deficits in episodic memory. More broadly, the present study adds to growing body of work investigating non-mnemonic functions of the hippocampus and reveals that whereas the hippocampus plays a critical role in some forms of linguistic processing, it is not always critical for qualitative aspects of language use at the single word level. The present results also suggest promising avenues for future work to further specify under what circumstances hippocampal processes or representations support language use and processing.

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Table 1.

Patient Demographic, Neuropsychological and Neurological Characteristics

Patient	Etiology	Age	Edu	WAIS III	WMS, III			Hipp	Subhipp
				VIQ	GM	VD	AD	Vol Loss	Vol Loss
P01	Encephalitis	55	14	92	45	56	55	73%	78%*
P02	Encephalitis	66	12	106	69	68	77	66%	72%+
P03	Anoxia/ischemia	60	12	83	52	56	55	N/A	N/A
P04	Anoxia + left temporal lobectomy	46	16	86	49	53	52	63%	60%^
P05	CO poisoning	54	14	111	59	72	52	22%	-
P06	Encephalitis	82	18	135	45	53	58	N/A	N/A
P07	Cardiac arrest	58	17	134	70	75	67	N/A	N/A
P08	Cardiac arrest	60	16	110	62	68	61	N/A	N/A
P09	Stroke	55	18	119	67	75	55	58%	-

Note. Age = Age (years); Edu = Education (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 Vol Loss = Bilateral Hippocampal Volume Loss; Subhipp Vol Loss = Parahippocampal Gyrus Volume Loss; CO = carbon monoxide

* = volume loss in bilateral anterior parahippocampal gyrus and left posterior parahippocampal gyrus.

+ = volume loss in bilateral anterior parahippocampal gyrus and right posterior parahippocampal gyrus.

^ = volume loss in left anterior parahippocampal gyrus.

Figure 1. Imageability Ratings in Experiments 1 and 2

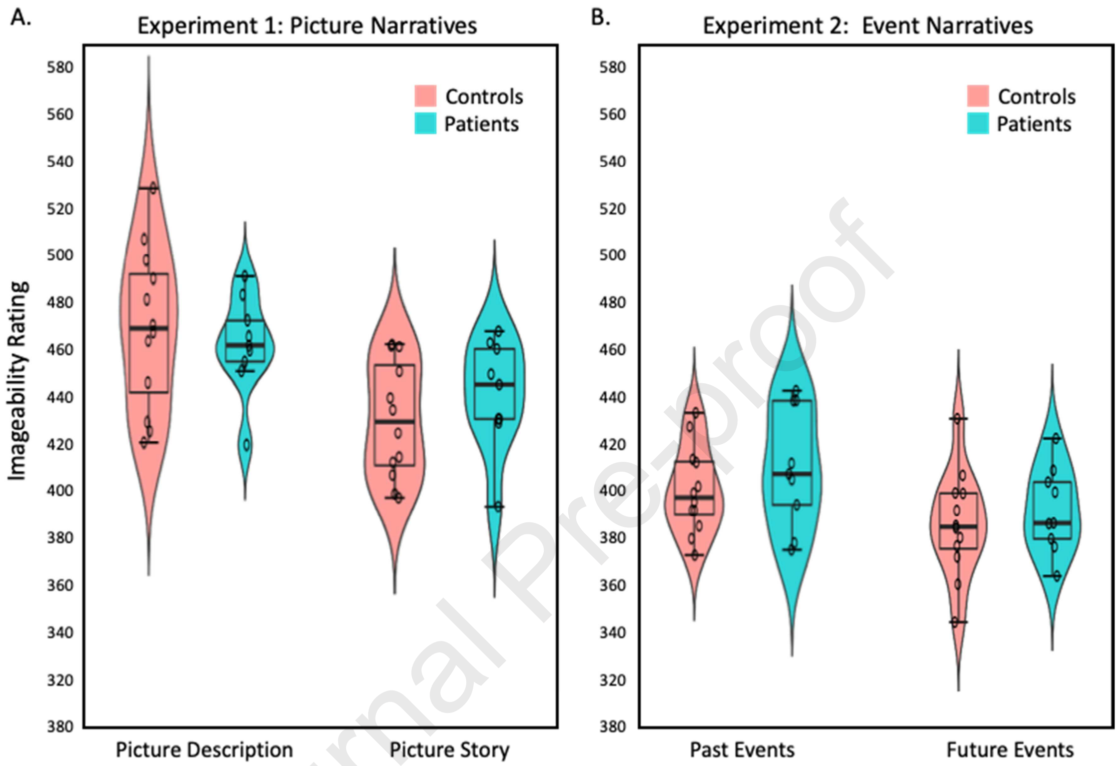

Figure 1. Average imageability ratings of words produced in (A) picture narratives (Experiment 1) and (B) event narratives (Experiment 2). Healthy controls (pink) and amnesic patients (blue) produced individual words rated similarly in imageability across all types of narratives. Boxplots depict median value, interquartile range, and minimum/maximum values. Violin plot depicts smoothed distribution curve. Circles represent individual participant data within each group.

Supplement

Supplementary Table 1

Distribution of Imageable Words in Experiment 1 and Experiment 2

	Quartile of Imageability Rating				
	Q1	Q2	Q3	Q4	Q5
	Experiment 1: Picture Description				
Static					
Patient	8	7	7	7	7
Control	9	10	9	10	10
Dynamic					
Patient	6	7	7	7	9
Control	10	9	8	9	9
	Experiment 2: Future/Past Narratives				
Past					
Patient	4	4	4	5	4
Control	7	6	6	6	6
Future					
Patient	3	4	4	4	4
Control	7	6	6	6	6

Note. Average number of words in each quintile (Q1-Q5) of imageability ratings is reported separately for each group and each condition.

- The hippocampus has been proposed to support language production
- Amnesic patients can use imageable words during event construction
- Imageability performance is intact even when narratives are impoverished
- Hippocampus does not play an obligatory role in the use of imageable words
- Hippocampal contributions to word use can be dissociated from contributions to memory