Sensitivity of the hippocampus to objective but not subjective episodic memory judgments

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Running Head: Subjective and objective recollection

Word count (main text including abstract and references): 3194

Figures: 2

Tables: 1

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Abstract

We assessed whether neural activity in the hippocampus dissociates according to whether memory test items elicit a subjective sense of recollection or accurate retrieval of contextual information. We reanalysed a previously acquired dataset from a study in which participants made both objective (source memory for spatial context) and subjective (Remember-Know) judgments for each test item. Results indicated that the hippocampus was exclusively sensitive to the amount of contextual information retrieved, such that accurate source memory judgments were associated with greater activity than inaccurate judgments, regardless of Remember/Know status. The findings add to the evidence that the hippocampus is insensitive to the subjective experience of recollection, but supports retrieval of contextual information.

Keywords

Episodic memory, recollection, familiarity, source memory, remembering, remember-know, fMRI

Introduction

Episodic memory refers to memory for unique events (Tulving, 1985). Two laboratory-based memory tests have frequently been employed to examine the role of the hippocampus in episodic recollection. One test requires participants to make an explicit judgement about a specific contextual feature of the study episode associated with a recognized test item (a source memory judgment). The other is the 'Remember/Know' procedure (Tulving, 1985), where participants are required to discriminate between test items associated with retrieval of any qualitative information about the study episode (Remember) and items recognized solely on the basis of an acontextual sense of familiarity (Know).

Despite the strong correlation between measures of recollection derived from these two test procedures (e.g. Alghamdi & Rugg, 2020), some fMRI studies have reported that hippocampal activity dissociates according to which test was employed to operationalize recollection (e.g., Slotnick, 2010; Yu, Johnson, & Rugg, 2012a; Rugg et al., 2012). For example, in Yu et al., (2012a), participants studied pictures presented to the left or right of fixation. In a later test phase, participants underwent fMRI while studied and unstudied pictures were presented in central vision. On each test trial, participants first made a Remember, Know, or New judgment. For each picture judged Remember or Know, they then signalled the item's study location using a 6-point confidence scale (ranging from 'highly confident left' to 'highly confident right'). Hippocampal activity was graded as a function of the accuracy and confidence of the source judgments associated with a Remember response. Hippocampal activity did not,

however, differ between Remember responses associated with the lowest level of source confidence and Know responses.

A limitation of the findings from Yu et al. (2012a) is that Remember responses associated with the lowest level of source confidence comprised a mixture of trials associated with accurate and inaccurate source judgments, thus confounding source accuracy with the subjective experience of 'Remembering'. This was also the case for the 'Know' response category, which comprised both accurate and inaccurate source responses.

Here, we reanalysed the Yu et al. (2012a) dataset to provide a novel test of the hypothesis that the hippocampus is sensitive to the amount of retrieved contextual information rather than the subjective experience of recollection. We collapsed across source confidence judgments and formed four response categories to orthogonalize the constructs of 'subjective' and 'objective' recollection: remember-accurate source, remember-inaccurate source, know-accurate source, and know-inaccurate source (cf., Hicks, Marsh, & Ritschel, 2002; Slotnick, 2010). We then examined whether the know-accurate source response category elicited greater hippocampal activity than the remember-inaccurate source response category. In contrast with the analysis conducted in Yu et al., (2012a), this analysis allows characterization of the neural activity associated with the accurate contextual retrieval in the absence of the subjective experience of 'Remembering'. The presence of a recollection effect for Know judgments would constitute strong evidence that hippocampal activity is driven by contextual retrieval independently of any accompanying phenomenal experience.

Method

Participants

The methods are described below in abbreviated form; see Yu et al., (2012a) for full details. Eighteen of the 23 right-handed, healthy young adults (14 females; age range 18-23 years, mean of 20 years) employed in Yu et al. (2012a) were included in the analyses below (participants in the currently reported analyses had a minimum of three trials in one or more of the four response categories described below). We note that when a stricter criterion of a minimum of 8 trials was employed, leaving a sample size of 10 participants, the same pattern of results was observed. Prior to participating, subjects gave informed consent in accordance with the University of California, Irvine, Institutional Review Board guidelines.

Procedure

At study, participants viewed 150 colored pictures of everyday objects presented sequentially either in the left or right visual field. Participants judged whether the depicted object would more likely be found indoors or outdoors on each study trial. Following the study phase, participants entered the MRI scanner prior to the test phase. This comprised 3 scanning runs. In each run, 50 old and 25 new pictures were randomly intermixed and presented at fixation with a stimulus-onset-asynchrony of 5.5 s. Each test run also comprised 25 randomly intermixed null trials. On each test trial, participants first made a Remember/Know/New response. Instructions were to use the Remember response option if recognition was associated with retrieval of any detail about an item's study presentation, to use the Know response for items judged studied in the absence of retrieval of any detail about the study episode, and to respond New to

items judged unstudied or when study status was uncertain. For each item judged Remember or Know, a second response cue appeared to signal the need for a source judgment (whether the item had been presented to the left or right of fixation at study). The judgment was made using a 6-point confidence scale (high, moderate, or low for each spatial location). One of six responses could be made depending on the confidence of the location judgment: 'Definite left' (referred to as 'high source confidence'); 'Probable left' (i.e., 'moderate source confidence'); 'Possible left' (i.e., 'low source confidence'); 'Definite right'; 'Probable right'; 'Possible right.' We collapsed over spatial location and source confidence for the analyses reported below.

fMRI acquisition and analysis

MRI data were acquired with a 3 T Philips Achieva scanner (Philips Medical Systems, Andover MA) equipped with an 8-channel SENSE head coil. Both T1-weighted anatomical images and T2*-weighted echoplanar images (TR of 2 s; 3 x 3 in-plane resolution, 1 mm gap, 30 slices, oriented parallel to the AC-PC line) were acquired. fMRI data were analyzed with Statistical Parametric Mapping (SPM8). Preprocessing included slice-time correction, two-pass spatial realignment, normalization into Montreal Neurological Institute (MNI) space (using the SPM8 EPI TPM template with resampling to 3 mm isotropic voxels) and smoothing with an 8 mm FWHM Gaussian kernel. Prior to analysis, functional timeseries were concatenated across the three test runs.

Univariate analysis was conducted on the preprocessed functional data in a two-stage mixed effects general linear model. In the first stage, each participant's BOLD response was modeled for each test item with a delta function at stimulus onset. The

design matrix comprised 4 events of interest: remember-accurate source trials, know-accurate source trials, remember-inaccurate source trials, and know-inaccurate source trials (mean number of trials ± 1 standard error of the mean: 70.06 ± 3.80, 30.06 ± 4.16, 20.56 ± 3.61, and 13.44 ± 1.90, respectively). A single additional event of no interest comprised new items, misses, false alarms, and missed test responses. The design matrix also included regressors for movement and a constant modelling each scan session

Participant-specific parameter estimates for the 4 events of interest were carried forward to a second analysis stage where they were entered into a repeated measures ANOVA with participants modeled as a random effect. To identify hippocampal regions of interest (ROIs) for further analysis we identified clusters demonstrating a main effect of Response Category (height thresholded at $p < 0.005$) in a manner that was unbiased with respect to each participant. Thus, we identified participant-specific ROIs via a leave-one-participant-out iterative procedure. For each participant, a hippocampal ROI was delineated by identifying hippocampal clusters demonstrating the aforementioned main effect of Response Category from the data of the remaining 17 participants. The ROI was confined to an anatomical mask of the hippocampus created by manually tracing the hippocampus on the across participant averaged T1 structural image. This approach ensured that for each participant, the pattern of activity within their hippocampal ROI was independent of the data used to identify it (cf. Kriegeskorte, Simmons, Bellgowan, & Baker, 2009).

Parameter estimates were extracted from 3 mm radius spheres centered around the peak hippocampal voxel of each participant's ROI. Pairwise contrasts were then

conducted to examine the data for differences due to source accuracy and the Remember vs. Know distinction. The mean peak MNI coordinate for the hippocampal ROI was: 29 -9 -25, with a mean (± 1 standard error) size of 13 ± 2 voxels.

Results

Table 1

	Source Accurate		Source Inaccurate	
	Remember	Know	Remember	Know
Confidence	2.43 (0.06)	1.58 (0.07)	2.03 (0.11)	1.39 (0.06)
Accuracy	78.7 (0.03)	68.0 (0.02)		

Mean source accuracy and confidence (± 1 standard error of the mean) for each of the four response categories. Confidence ranging from 3 (high), 2 (moderate), and 1 (low).

Table 1 lists the average confidence rating (± 1 standard error of the mean) associated with each of the four response categories. Pairwise t-tests revealed that remember-accurate source responses were associated with greater confidence than all other response categories (ts(17) > 5.77, ps < 0.001, Cohen's ds > 1.36). Know-accurate source responses were associated with greater source confidence than know-inaccurate source responses (ts(17) = 3.51, p < 0.01, d = 0.83). Lastly, remember-inaccurate source responses were associated with greater confidence than know-inaccurate and accurate source responses (ts(17) > 3.34, ps < 0.01, ds > 0.79). Source accuracy (Table 1) for Remember responses was higher than for Know responses (t(17) = 4.90, p < 0.001, d = 1.12); both measures were however greater than chance (ts(17) > 8.76, ps < 0.001, ds > 1.96; one-tailed).

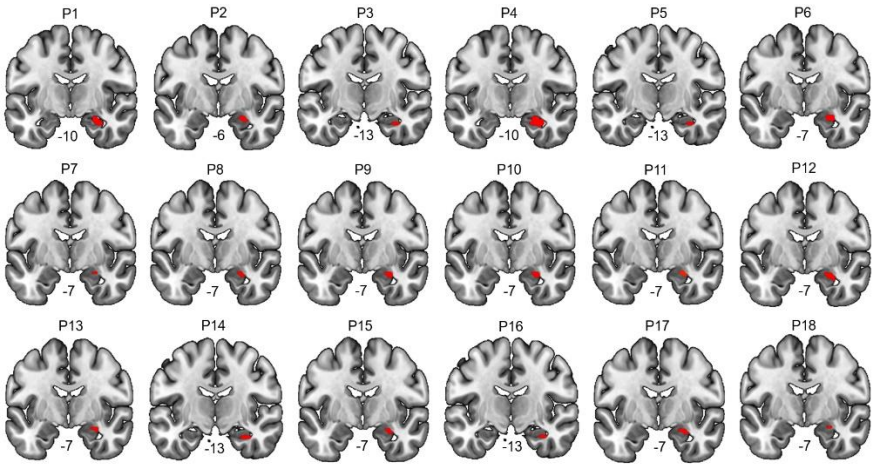

Figure 1. Individual participants' hippocampal ROIs displaying the coronal slice (MNI Y coordinate listed below) on which the peak hippocampal voxel was identified.

Figure 1 illustrates the participant-specific hippocampal ROIs delineated by identifying hippocampal clusters demonstrating the aforementioned main effect of Response Category from the data of the remaining participants.

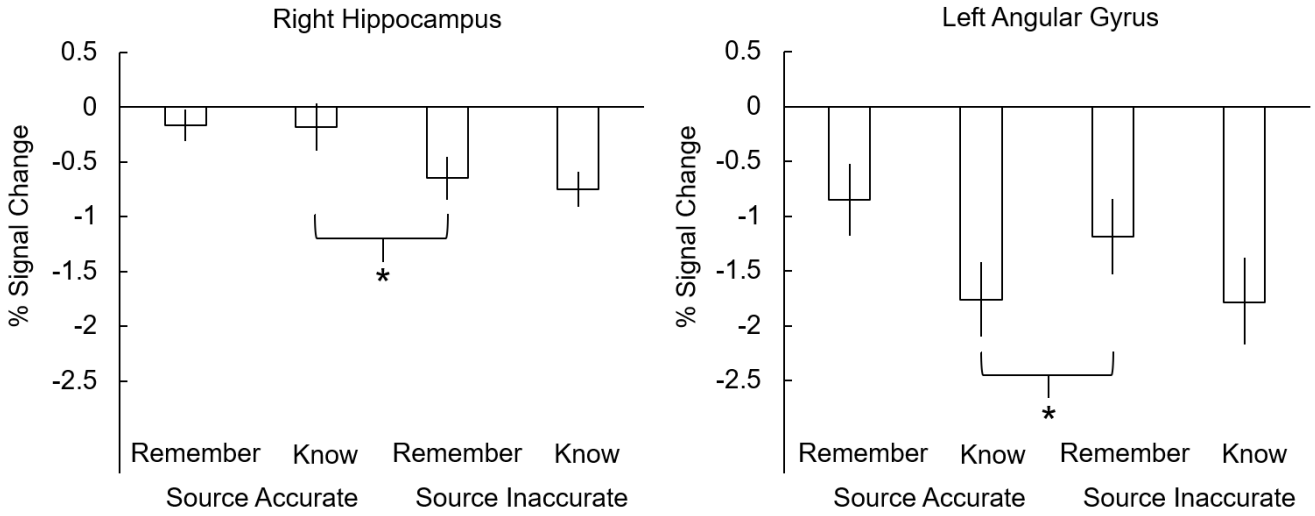

Figure 2. Mean parameter estimates (± 1 standard error of the mean) extracted from a 3 mm sphere centered around the peak voxel within the hippocampus (left) and the left angular gyrus (right).

Figure 2 (left) depicts the parameter estimates extracted from the hippocampal ROI. Crucially, in line with the prediction that the hippocampus would be sensitive solely to the amount of retrieved contextual information, parameter estimates for Know

judgments associated with accurate source responses were significantly greater than those for Remember judgments associated with inaccurate responses ($t(17) = 2.21$, $p < 0.05$, $d = 0.52$). In contrast to prior data reporting a similar effect (Slotnick, 2010), the present finding cannot be attributed to a difference in the strength of source memory (as operationalized by response confidence) since Remember-inaccurate judgments were associated with significantly greater confidence than were Know-accurate responses.

Additional pairwise comparisons on the parameter estimates from the hippocampal ROIs revealed that source accurate responses tended to be associated with greater hippocampal activity than source inaccurate responses for both Remember ($t(17) = 2.90$, $p < 0.05$, $d = 0.68$) and Know responses ($t(17) = 2.04$, $p = 0.06$, $d = 0.48$). Hippocampal activity did not significantly differ between Remember and Know responses for either accurate or inaccurate source judgments ($ts < 1$).

To assess whether the hippocampus was unique with respect to its sensitivity to contextual retrieval rather than subjective recollection, we compared the pattern of neural activity in the hippocampus with that in the left angular gyrus. We chose the left angular gyrus because, among its many other functions - which seemingly include supporting the retrieval of contextual information (e.g., Vilberg & Rugg, 2007; Yu et al., 2012b; for a review, see Rugg & King, 2018) - the region has been reported to contribute to the subjective experience of recollection (for a review, see Simons, Ritchey, & Fernyhough, 2022). The left angular gyrus ROI was identified in the same manner as the hippocampal ROI (i.e., a leave-one-participant-out iterative procedure). The mean peak MNI coordinate for the ROI was: -44 -75 -26, with a mean (± 1 standard error) size of 595 ± 222 voxels. Figure 2 (right) depicts the parameter estimates

extracted from this ROI. Along with the corresponding estimates from the hippocampus, these were entered into a 2 (Region) x 4 (Response Category) ANOVA. In addition to significant main effects of Region and Response Category (Fs > 6.69, ps < 0.05, partial η^2 > 0.28), the ANOVA revealed a significant Region by Response Category interaction ($F(2.78, 47.19) = 5.11$, $p < 0.01$, partial $\eta^2 = 0.23$). In a striking contrast to the pattern observed in the hippocampus (see above), a follow-up paired t-test revealed that, in the angular gyrus, Remember judgments coupled with inaccurate source responses were associated with significantly greater BOLD activity than were Know judgments coupled with accurate responses ($t(17) = 2.49$, $p < 0.05$, $d = 0.59$).

Additional pairwise comparisons on the parameter estimates from the angular gyrus ROIs revealed that Remember responses tended to be associated with greater activity than Know responses for both accurate ($t(17) = 4.75$, $p < 0.001$, $d = 1.12$) and inaccurate source responses ($t(17) = 2.24$, $p < 0.05$, $d = 0.53$). However, when Remember and Know judgements were compared as a function of source accuracy (i.e., remember source accurate responses versus remember source inaccurate responses, and analogously for Know judgments), no significant differences were observed (ts < 1.72, ps > 0.10).

Discussion

The aim of the present study was to assess whether hippocampal activity dissociates according to whether recognition memory test items elicit subjective or objective evidence of successful recollection. Thus, we examined whether hippocampal activity was elevated for accurate source memory judgments made on test items rated

as familiar only in comparison with inaccurate judgments made on items rated as remembered. The former class of judgments were associated with reliably greater hippocampal activity. These findings are consistent with prior reports that retrieval-related hippocampal activity is driven by contextual retrieval rather than the phenomenal experience typically associated with successful episodic retrieval (Slotnick, 2010; Rugg et al., 2012; Yu et al., 2012a; Richter, Cooper, Bays, & Simons, 2016).

Of importance, these hippocampal contextual retrieval effects were not shared with at least one other member of the 'core recollection network' (Rugg and Vilberg, 2013), namely, the left angular gyrus. In contrast with the hippocampus, test items attracting Remember judgments elicited greater activity than did items endorsed Know, regardless of source accuracy. These findings are consistent with prior evidence demonstrating the sensitivity of the angular gyrus to the subjective experience of recollection (for a review, see Simons et al., 2022). The present findings for the angular gyrus might appear to contradict our previously reported analysis of the same data, which indicated that, like the hippocampus, the region is sensitive to the retrieval of contextual information (Yu et al., 2012b). The seeming disparity between the current findings and those reported by Yu et al. (2012b) reflect the fact that in the prior analysis neither Remember or Know judgments were segregated according to source accuracy (notably, Remember-low confidence and Know-low confidence response categories each comprised a mixture of accurate and inaccurate responses). Consistent with the findings of Yu et al. (2012b), however, the present analyses again demonstrated that, in the angular gyrus, items attracting Remember but source inaccurate judgments elicited larger BOLD responses than items attracting analogous Know judgments.

The present hippocampal effects were right lateralized, while those reported by Yu et al. (2012a) were left-lateralized. As just discussed in respect of the angular gyrus, this divergence likely also reflects the differing analytical approaches taken in the prior and present studies. Yu et al. (2012a) focused on identifying hippocampal clusters where activity varied as a function of Remember responses that were associated with differing levels of source confidence. The current analysis was directed toward the identification of clusters that demonstrated a main effect across all four response categories of interest. Regardless of the difference in localization, the present findings converge with those of Yu et al. (2012a) in indicating that retrieval-related hippocampal activity covaries with amount of retrieved contextual information (for additional analyses aimed to determine whether the present results were mirrored in the left hemisphere, and also to compare the findings with those reported in Yu et al., (2012a), see Supplemental Online Material).

The current findings are limited to objective and subjective indices of episodic memory as these are operationalized by source memory and Remember/Know procedures, respectively. It will be important for future studies to determine whether the present findings extend to other operationalizations of objective and subjective recollection (e.g., associative memory and vividness), and to recollection of contextual features other than spatial location. Nonetheless, the present findings support models of hippocampal function that propose that the role of the hippocampus is to bind item and contextual information into a memory representation that supports later episodic recollection (e.g., Diana, Yonelinas, & Ranganath, 2007).

Funding

This work was supported by the National Institute of Mental Health [grant number R01-MH072966] to M.D.R.

Disclosure of interest

The authors report no conflict of interest.

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Supplemental Online Material

fMRI results.

To determine whether the present results were mirrored in the left hemisphere, and also to compare the findings with those reported in Yu et al., (2012a), we performed to additional analyses. First we extracted parameter estimates from a homologous left hippocampal ROI in each individual participant. In addition, we extracted parameter estimates from 3 mm spheres centered on the peak left hippocampal voxel reported in Yu et al., (2012a: MNI co-ordinates of -30 -16 -20). Regardless of which parameter estimates were employed, ANOVA's with factors of Hemisphere and Response Category failed to identify any evidence for a Hemisphere by Response Category interaction ($Fs < 2.82$, $ps > 0.05$). These null findings might be taken to suggest that the present findings for the right hippocampus are comparable both across hemispheres, and with those those reported in Yu et al. (2012a). However, after collapsing the data across hemispheres, the pairwise comparison between Remember judgments associated with inaccurate source responses and Know judgments associated with accurate source responses was not significant. These findings are therefore are ambiguous as to whether or not there is a qualitative difference in the pattern across hemispheres.