

Short communication

The anterior medial hippocampus contributes to both recall and familiarity-based memory for scenes

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ABSTRACT

The hippocampus is usually associated with recall memory, whereas its contribution to familiarity-based memory is debated. Growing evidence support the idea that this structure participates to any cognitive process performed on scene representations. In parallel, differences in functional specialisation and cortical connectivity were found across the longitudinal and transverse axes of the hippocampus. Here we reanalysed functional MRI data from 51 participants showing stronger engagement of the hippocampus in recall, familiarity-based recognition and rejection, and visual discrimination, of scenes compared to single objects. A conjunction analysis between these four tasks revealed a set of occipital, medial temporal, posterior cingulate, and parietal regions, matching the scene construction network described in the literature. Crucially, we found that the anterior medial part of the hippocampus was consistently involved in all tasks investigated for scene stimuli. These findings support that the hippocampus can contribute to both recall and familiarity-based memory, depending on stimulus type. More generally, this bolsters the recent proposal that circumscribed regions within the hippocampus may underpin specific cognitive mechanisms.

1. Introduction

The hippocampus (HC) is a key structure of human behaviour as it has been associated with memory (Squire, 1992), spatial cognition (Moscovitch et al., 2006), language (Duff & Brown-Schmidt, 2012), creative thinking and problem solving (Warren et al., 2016), and decision making (Dickerson et al., 2011). In the domain of memory, the HC is traditionally believed to be responsible for the process of recollection, which involves the rich and contextualised retrieval of an episode (Yonelinas, 2002). In contrast, there has been a longstanding debate regarding the contribution of this structure to familiarity memory, defined as the simple feeling that a stimulus has been encountered before. While some authors have claimed that familiarity is independent of the HC (Eichenbaum et al., 2007), others have argued that this region supports both recollection and familiarity memory (Gold et al., 2006).

One influential proposal to resolve this discrepancy is to examine what is retrieved, namely the memory content (Mayes et al., 2007; Saksida & Bussey, 2010). Cumulative evidence showed that the HC is involved in the processing of spatial scenes in memory but also non-memory processes such as future thinking (Addis et al., 2007),

imagination (Hassabis et al., 2007; Mullally et al., 2012) and visual perception (Hodgetts et al., 2017; McCormick et al., 2021; Zeidman et al., 2015). This evidence has converged towards the idea that the HC contributes to various domains of cognition through a common mechanism: the construction of spatial scenes (Maguire & Mullally, 2013). In line with this model, we recently showed that the HC is more engaged in recall memory, but also familiarity-based recognition and rejection, for scenes than for objects (Gardette et al., 2022). Importantly, these findings support that the HC can play a role in both recall and familiarity-based memory depending on memory content.

Research have showed that the HC should not be considered as a unitary structure, as internal differences in functional specialisation have been described (Strange et al., 2014). In particular, the sharpness with which information is represented seems to increase gradually along its anterior-posterior axis (Brunec et al., 2018; Poppenk, 2020; Poppenk et al., 2013). More recently, research has also revealed that the HC cortical inputs/outputs vary both along its longitudinal and transverse axes (Dalton et al., 2022). Neurons of the posterior-medial HC connect preferentially to visual and other sensory areas, whereas neurons of the anterior-lateral HC are more connected with semantic areas (i.e.,

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inferior lateral temporal cortex). In addition to these gradients of connectivity, Dalton and colleagues showed that the anterior-medial HC (amHC) is particularly connected with temporal, medial parietal, and occipital regions. Crucially, several functional magnetic resonance imaging (fMRI) studies have previously associated amHC activity with various cognitive tasks that imply the construction of a spatial scene (Addis et al., 2012; Dalton et al., 2018; Hodgetts et al., 2017; Lee et al., 2013; Zeidman et al., 2015). These results provide important insights into the functional organization of the HC, and lead to the question of the potential specialisation of different HC sub-regions in memory processes. Because this question was not among our preregistered hypotheses, we did not directly explore whether recall and familiarity-based memory processes were associated with a same or different sub-regions of the HC in our previous study (Gardette et al., 2022). Considering emerging evidence that the amHC plays an important role in scene-based cognition, we hypothesised that this region would be commonly recruited across recall, familiarity-based memory, and visual perception of scene stimuli (i.e., the encoding task). To this end, as was done in previous studies investigating similar questions (e.g., Zeidman et al., 2015), we performed a conjunction analysis between the four tasks performed on scenes and objects. This analysis allowed us to test the hypothesis that a set of brain regions including the amHC was consistently recruited for the processing of scene stimuli, irrespective of the nature of the process engaged (Friston et al., 2005).

2. Methods

We reanalysed the data presented in Gardette et al. (2022). The original study was approved by the National French Ethics Committee for the Protection of Human Subjects (CHUGA promotion; CPP 2020-A01592-37; ClinicalTrials ID NCT04562974).

2.1. Participants

Fifty-one healthy young participants participated (mean age $M = 21.3$, $SD = 2.1$, 13 males). All participants had normal or corrected-to-normal vision, and none had any neurological or psychiatric condition.

2.2. Procedure

Participants first completed a visual matching task, also constituting the encoding task for the subsequent memory test. In this task, three stimuli are presented simultaneously on screen, and participants are asked to determine which of the two lower stimuli matches the one above (Fig. 1.A). Subsequently, 25 participants performed a patch-cued reconstruction task measuring pattern-completion like retrieval (Fig. 1. B, see Ross et al., 2018). In this task, circular patches displaying limited portions of the original stimuli are presented to the participants who are instructed to mentally reconstruct the original images. Therefore, trials in which participants correctly responded “reconstruction” are regarded as pattern-completion like retrieval, a mean of measuring recall memory of different classes of stimuli. The 25 remaining participants performed a traditional remember/know paradigm (Fig. 1.C; Rajaram, 1993; Tulving, 1989). In this task, they are presented with old and new stimuli in the same form as during encoding, and are asked to specify whether they specifically remember seeing the stimulus before (i.e., recollection), whether the stimulus only feels familiar to them (i.e., familiarity-based recognition), or whether they think the stimulus is new (i.e., familiarity-based rejection). Trials in which participants correctly responded “familiar” and “new” were analysed to measure familiarity-based memory.

2.3. Material

In all tasks, scene and object stimuli were used and constitute the variable of interest in the present study (i.e., [Scene – Object] contrast).

All images were greyscale and low-level visual properties of images were equalised between objects and scenes. For full details of the material construction, readers are referred to the original study (Gardette et al., 2022).¹ In keeping with the methodology used by Ross and colleagues (2018), patches were 150-pixels diameter circular windows cropped from the encoded images. Their position in the original images was chosen in order to display enough features to make reconstruction possible, but to avoid displaying critical elements that would make recognition too easy.

2.4. Analyses

In the original study, anatomical regions of interest (ROI) of the HC and perirhinal cortex were drawn on each subject’s native structural MRI scan, and fMRI signal was extracted from these masks. This procedure did not allow to reveal the precise location of the region within the HC that responded to scene processing, since data were not normalised and thus not comparable between subjects. In this reanalysis, images were first realigned and co-registered, the anatomical T1 scan of each participant was then segmented and normalised to the Montreal Neurological Institute (MNI) template using SPM 12 (<https://www.fil.ion.ucl.ac.uk/spm/>). Functional volumes were then normalised using the parameters derived from the anatomical normalisation step, and smoothed using a 3-mm FWHM Gaussian kernel. A high-pass filter (1/128 Hz cut-off) was finally applied. Statistical parametric maps generated at the individual level with the [Scene – Object] contrast were entered into a one-way Anova for each task (i.e., Pattern-completion, familiarity-based recognition and rejection, and visual matching), constituting the between-subject conjunction analysis aiming to identify the regions commonly activated across the four conditions. The conjunction null hypothesis test was used (i.e., instead of the global null hypothesis, Nichols et al., 2005), corresponding to a logical “and” between the results of each contrast. Considering the over-conservative false positive rate of this analysis (Friston et al., 2005), an uncorrected peak level threshold of $p < .001$ was applied to the results.

3. Results

The conjunction analysis for scenes versus objects revealed a limited set of activated regions in the bilateral medial temporal, occipital, and cingulate cortices, as well as right HC. Given the selected conjunction procedure implemented in SPM (see methods section), those regions consistently responded to the contrast scene processing relative to object processing in the four conditions investigated. The regions activated are listed in Table 1. The reverse contrast (i.e., Object – Scene) only revealed one activated cluster in the right posterior fusiform gyrus (peak MNI coordinates 48, –58, –15).

The main goal of the present study was to identify the region within the HC that contributed to both recall and familiarity of scenes in the original study. As expected, the cluster commonly activated for scene processing within the HC was located in the anterior-medial region. The peak MNI coordinates (i.e., 21, –18, –18) also matched those reported in the literature (i.e., 22, –20, –18, in Zeidman & Maguire, 2016). Moreover, as illustrated in Fig. 2, this region was strikingly close to that described recently by Dalton et al. (2022). Yet, based on the conjunction analysis, it cannot be ruled out that one task engaged the amHC more than the others. We therefore conducted an exploratory analysis comparing the activity for the [Scene – Object] contrast in the amHC region between the three tasks with comparable experimental designs (i.e., recall, familiarity, and new judgement). This analysis revealed no significant difference between the three tasks (see supplementary analysis 1 and figure S1).

¹ The material and data from the original study are available at: https://osf.io/3869n/?view_only=2eaedc798b6c4820ad3db0ac69e916d0.

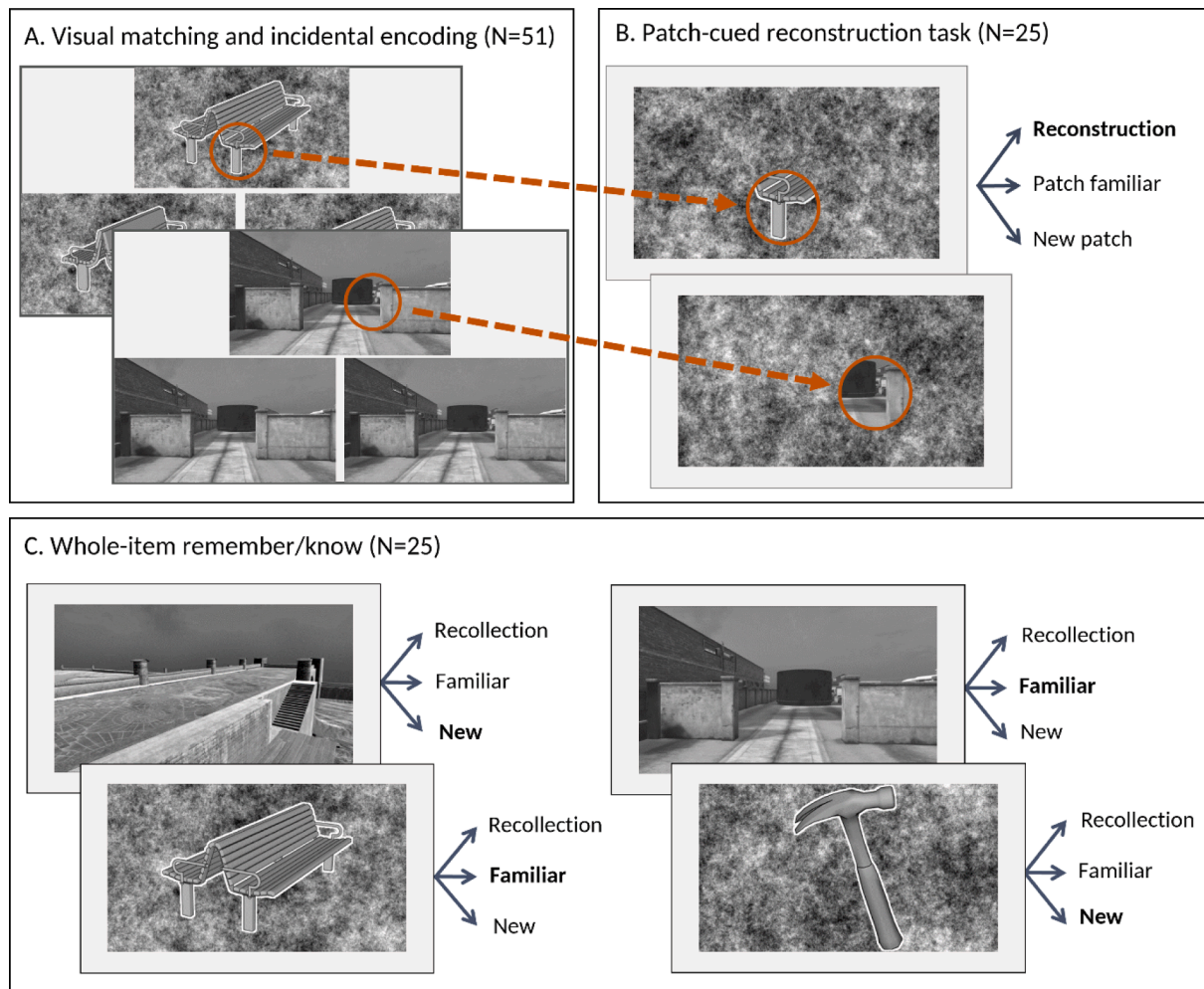


Fig. 1. Illustration of the four tasks investigated, in the scene and object conditions. (A) Visual matching and incidental encoding: Participants were instructed to determine which of the stimuli presented below matches the one above. (B) Patch-cued reconstruction: Participants were asked to try mentally reconstructing the original images; correct “Reconstruction” trials were analysed as *pattern-completion*. (C) Whole-item remember/know: Participants indicated for each stimulus whether they specifically remembered seeing it before (“Recollection”), they found it familiar (“Familiar”), or they thought the image was new (“New”). Correct “Familiar” and “New” trials were analysed as *familiarity-based recognition and rejection*, respectively. Note: although 51 participants were included in the analyses of the matching task, only 50 participants could be included in the analyses of the recognition tasks due to performance-related inclusion criteria.

Table 1

Results of the conjunction analysis testing the Scene – Object contrast in the four tasks ($p < .001$ uncorrected), minimum extent 2 voxels. For each, the number of voxels (K), T value, MNI coordinates, and AAL3 label (Tzourio-Mazoyer et al., 2002) are given. The hippocampus cluster is in bold. Note: Only the first cluster survived a threshold of $p < .05$ family-wise error (FWE) corrected.

K	T	Coordinates (X, Y, Z)	Region (AAL3)
82	5.29	-21, -42, -12	Left Parahippocampal gyrus
	3.30	-26, -50, -5	Left Lingual gyrus
14	4.27	24, -36, -15	Right Parahippocampal gyrus
81	4.19	33, -38, -12	Right Parahippocampal gyrus
	4.04	30, -48, -6	Right Lingual gyrus
19	3.99	14, -48, 3	Right Precuneus
2	3.84	-24, -35, -21	Left Fusiform gyrus
7	3.78	21, -18, -18	Right Hippocampus
7	3.75	8, -47, 5	Right Posterior cingulate gyrus
5	3.68	-32, -38, -14	Left Parahippocampal gyrus
7	3.67	24, -86, -12	Right Fusiform gyrus
3	3.39	-14, -95, -3	Left Calcarine sulcus

4. Discussion

In this study, we conducted a reanalysis of the data from our recent article which reported an increase in HC activity for recall, familiarity-based recognition and rejection, and visual perception of scenes, compared with objects (Gardette et al., 2022). Specifically, we sought to determine whether a same region of the HC was engaged in these four conditions. To this aim, a conjunction analysis was performed on normalised data to identify the voxels that were consistently activated by scene processing compared to object processing across all tasks. This analysis revealed a set of activated regions in the medial and inferior temporal, parietal, posterior cingulate, and occipital lobes. These regions match the scene construction network described in previous studies (Dalton et al., 2018; McCormick et al., 2021; Zeidman et al., 2015). Although task difficulty cannot be properly dissociated from material type in the present study and could constitute an alternative explanation of our results, there is evidence that this network, including the anterior HC, responds to scene construction irrespective of complexity (McCormick et al., 2021). We therefore interpret these findings as meaning that participants constructed/reconstructed spatial scene representations in all task conditions.

The main goal of this study was to investigate the region within the

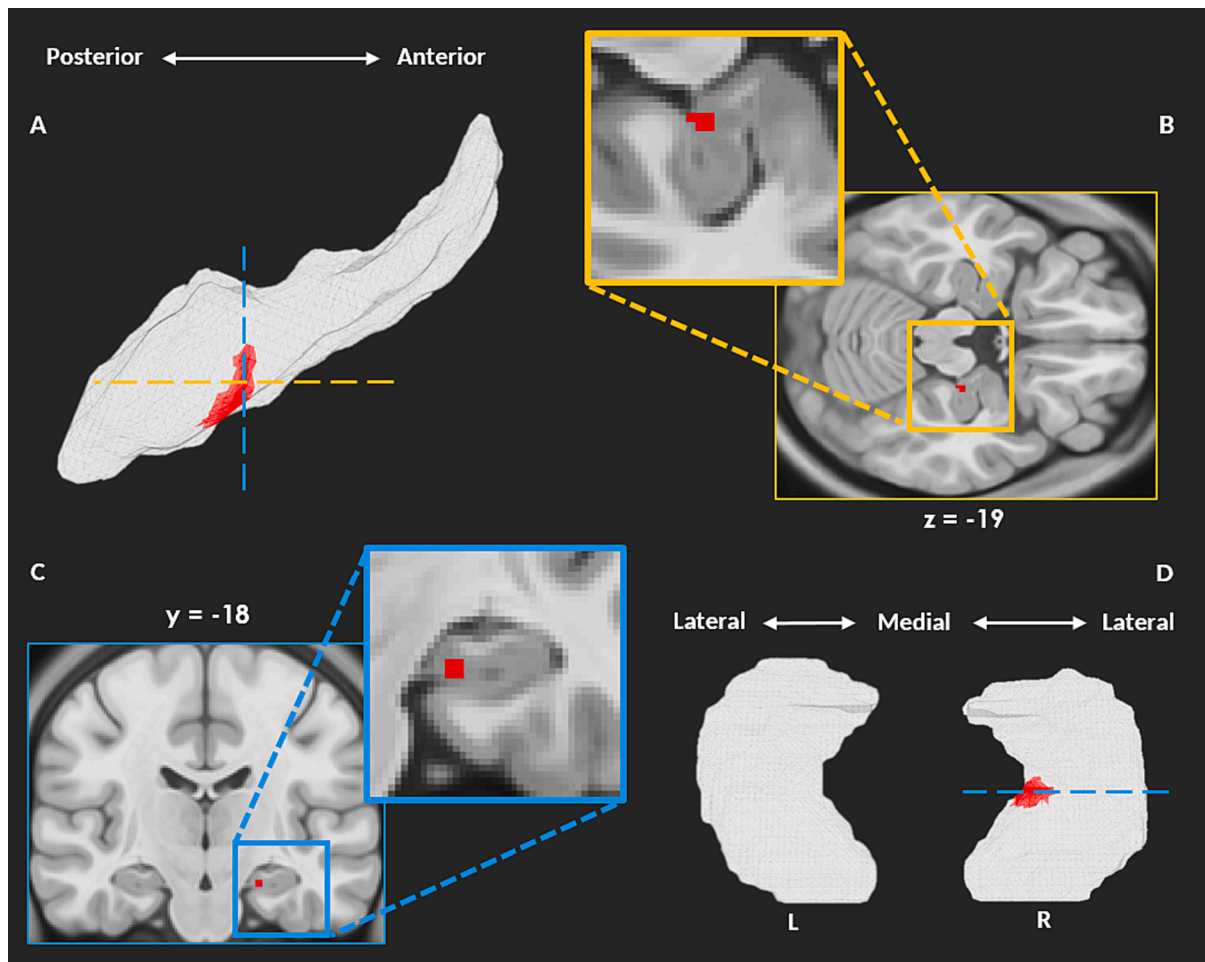


Fig. 2. Significant activation resulting from the conjunction analysis within the hippocampus. The region is projected on 3-dimensional rendering of the hippocampus based on the Brainnetome atlas (Fan et al., 2016), presented from medial (A) and ventral (D) views. The cluster position is represented on axial (B) and coronal (C) slices using the ICBM152 T1 template (Fonov et al., 2009, 2011).

HC that would contribute to scene processing across the tasks. As expected, this region was located in the anterior-medial portion of the HC. This result is consistent with previous studies that have identified the role of the amHC in scene recall (Addis et al., 2007, 2012; McCormick et al., 2015) and visual perception (Hodgetts et al., 2017; Lee et al., 2013; Zeidman et al., 2015). Showing that this region is also engaged in familiarity-based recognition, and rejection, in contrast, is a new result. As mentioned, whereas some studies have linked the HC with both familiarity and recollection (Wais et al., 2010), most have failed to find HC activity for familiarity-based memory (for review see Diana et al., 2007). Yet, patients with circumscribed lesions of the HC are impaired in recognition tasks for scene stimuli (Bird et al., 2007; Taylor et al., 2007). Crucially, such impairments were found for both recollection and familiarity when using a process-dissociation procedure (Cipolotti et al., 2006). Manipulating representational content (i.e., scenes versus objects) is thus critical to unravel the contribution of medial temporal lobe regions to memory processes (Saksida & Bussey, 2010). Using the same manipulation, we further show that familiarity memory and new judgements for scenes specifically rely on the right amHC. Our findings are consistent with a case study by Irish and colleagues (2017) that evidenced impaired scene construction after lesions of the right anterior HC. Moreover, preserved scene construction abilities in case of amnesia were documented by Mullally et al., and was supported by the same region (2012). The right amHC would therefore support scene-based processing, independently of the cognitive process evaluated (Zeidman & Maguire, 2016).

As mentioned in the introduction section, differences in functional specialisation along the anterior-posterior axis of the HC have been widely reported both in non-human animals and humans (for review see Strange et al., 2014). More precisely, information seems to be represented at different scales, with sharper representations in the posterior HC and broader representations in the anterior HC (Brunec et al., 2018). It has been proposed that the anterior HC would represent any kind of broad information (Poppenk et al., 2013), including gist-like memories (Robin & Moscovitch, 2017), and global spatial layouts such as scenes (Evansmoen et al., 2013). In a recent study, Dalton and colleagues used density-based fibre tracking to reveal gradients of cortical connectivity both along the longitudinal and transverse axes of the HC, as well as circumscribed regions within the HC displaying particular patterns of cortical connectivity (Dalton et al., 2022). Temporal areas preferentially connect to the lateral portion of the anterior HC, whereas the amHC shows strong connectivity with a set of brain regions including medial parietal, ventral temporal, and occipital cortices. Crucially, the amHC region identified using this technique aligned with the amHC region identified in the human functional neuroimaging literature (i.e., located at the apex of the uncus, Zeidman & Maguire, 2016; Dalton et al., 2018). The location of the amHC cluster observed in the present study was strikingly close to that reported by Dalton et al. (Fig. 2). Yet, in these studies, the amHC region corresponded to the *pre/para*-subiculum, compared with which the region resulting from the conjunction analysis seems slightly offset. This discrepancy might be explained by the conservative nature of the conjunction null hypothesis approach, which

only reveals the regions strictly overlapping between the four tasks (Friston et al., 2005), as well as by methodological differences between previous studies and ours (e.g., template registration).

The medial HC could constitute a hub responsible for processing visuospatial information (Dalton & Maguire, 2017), the sharpness of which would correspond to global spatial representations such as scenes in the amHC, and to local representations such as sensory details in the posterior medial HC (Poppenk & Moscovitch, 2011; Robin & Moscovitch, 2017). Taken together, those results provide a novel framework for understanding how the HC contributes to various cognitive functions, including familiarity and recall memory.

CRedit authorship contribution statement

J. Gardette: Conceptualization, Methodology, Writing – original draft. **E. Cousin:** Methodology, Formal analysis, Software. **P. Hot:** Conceptualization, Resources, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data is fully available on the OSF. The link is in the article and will be copied in the appropriate step of the submission process.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.nlm.2023.107859>.

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