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# Hippocampal activity during memory and visual perception: The role of representational content

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### ABSTRACT

The functional organisation of the medial temporal lobe (MTL) has long been described on the basis of cognitive processes such as recollection or familiarity. However, this view has recently been challenged, and researchers have proposed decomposing cognitive phenomena into *representations* and *operations*. According to the representational view, representations, such as *scenes* for the hippocampus and *objects* for the perirhinal cortex, are critical in understanding the role of MTL regions in cognition. In the present study, 51 healthy young participants underwent functional magnetic resonance imaging (fMRI) while completing a visual-discrimination task. Subsequently, half of the participants performed a patch-cue recognition procedure in which “Rec” responses are believed to reflect the operation of pattern completion, whereas the other half performed a whole-item remember/know procedure. We replicated the previously-reported demonstration that hippocampal involvement in pattern completion is preferential for scenes as compared with objects. In contrast, the perirhinal cortex was more recruited for object processing than for scene processing. We further extended these results to the operations of strength-signal memory and visual discrimination. Finally, the modulation of hippocampal engagement in pattern completion by representational content was found to be specific to its anterior segment. This observation is consistent with the proposal that this segment would process broad/global representations, whereas the posterior hippocampus would perform sharp/local representations. Taken together, these results favour the representational view of MTL functional organisation, but support that this specialisation differs along the hippocampal long-axis.

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## 1. Introduction

The hippocampus is usually associated with recollection, the rich retrieval of a memory in its context, whereas the perirhinal cortex (PRC) is believed to underpin familiarity, or knowing that a stimulus has been encountered before without remembering any associated information (Aggleton & Brown, 1999, 2006; Moscovitch et al., 2006). However, a recent approach to memory investigation proposes to decompose processes such as recollection into *representations* and *operations* (Cowell et al., 2019). Representations refer to “patterns of neural firing, standing for elements of the environment – such as stimuli or events”. Operations refer to “algorithmic computations performed by the brain – such as the computation of the match between two signals” (further explanations in Cowell et al., 2019). The process of recollection is thus a combination of the operation of retrieval and the representation that is retrieved. The operation involved in recollection is a rich and detailed retrieval from few or no clues, termed *pattern completion*. Crucially, the definition of pattern completion adopted by Cowell, Sadil, and Barense is independent of the memory content to be retrieved (see also Taylor & Henson, 2012). The memory content retrieved during recollection is a complex, associative representation that includes a temporal and/or spatial context. In contrast, the process of familiarity involves the operation of generating a memory-strength signal and assessing its strength. Once again, this operation is independent of the memory content, or representation (Cowell et al., 2019). Notably, this view does not claim that recollection and familiarity do not exist, but argues that the functional organisation of the human brain is better understood through operations and representations than through complex, high-order, cognitive phenomena.

The interest in breaking cognitive processes into operations and representations is to consider the influence of one in isolation from the other. When characterising the functional organisation of medial temporal lobe (MTL) structures, the question emerges as to whether their specialisation depends on the operations or the representations. Specifically, does hippocampal engagement in recollection rely on the operation of pattern completion, or on the complex, associative representation that is retrieved? Thereby two hypothetical accounts emerge: one operation based and the other representation based (Ross et al., 2018; represented in Fig. 1). According to the operation-based hypothesis, MTL regions are functionally organised according to operations, irrespective of the representations. In this view, different brain structures are engaged by different operations (e.g., pattern completion, memory-strength signal generation), regardless of the representations processed. The hippocampus should thus be involved in the pattern completion of any representation, whereas pre-hippocampal regions should be recruited during other operations, such as the PRC for the memory-strength signal. In a representation-based hypothesis, similar MTL regions should be engaged for various operations as long as the representation is held constant. In contrast, different structures should respond to different representations (e.g., single objects, scenes). The hippocampus should therefore be involved in any operation performed on highly-complex associative representations, whereas pre-hippocampal regions should be engaged when other representations are being processed.

There is growing evidence in favour of the representational account, specifically the representational–hierarchical (RH) model of the ventral occipito-temporal stream and the MTL areas (Cowell et al., 2010; reviews in Bussey & Saksida, 2007; Graham et al., 2010; and Saksida & Bussey, 2010). The main assumption of this model is that the specialisation of these areas depends only on the nature of the stimuli processed, irrespective of the cognitive processes engaged. In other words, the representational content conveyed, not the operations performed on it, determine the brain structures recruited in a cognitive process. According to the RH model, the determinant characteristic of a memory is its *dimensionality*. Memory contents containing spatial, cross-modal, semantic, or arbitrary associations between elements, are considered *high-dimensional*, whereas memory contents comprising only single-object or object–object associations are *low-dimensional* (Cowell et al., 2019). The ventral visual stream would be hierarchically organised along the posterior–anterior axis, with posterior areas processing simple visual features and anterior regions processing representations of higher dimensionality. This organisation relies on *feature conjunction*, or the gradual binding of simple representations to create more complex representations (see Ross et al., 2018, for direct causal modelling evidence in support of this account). Visual features in occipital regions thus assemble to create simple shapes, which in turn assemble to create objects parts, whole objects, and eventually the complex representation of objects in a scene (Bussey & Saksida, 2007). Single-object representations are believed to rely on the PRC (Barense et al., 2005; Lee, Buckley, et al., 2005; Lee, Bussey, et al., 2005; see also Cowell, 2012). Representations processed by the PRC are then conveyed to the hippocampus, which integrates them into a scene. In this view, the hippocampus sits at the highest level of the hierarchy and processes representations of the highest dimensionality. These complex, hippocampal-dependent representations include spatial, temporal, and/or cross-modal associations (Cowell et al., 2019), these being the components usually associated with recollection.

Growing experimental evidence supports the representational account of hippocampal functions. Recollection and familiarity have been shown to be equally impaired for scenes, but not for single items, following isolated hippocampal lesions (Bird et al., 2007; Cipolotti et al., 2006; Taylor et al., 2007). Deficits for both scenes and single items have been reported in the presence of more extended lesions that include both the hippocampus and the PRC (Taylor et al., 2007). Further, impaired recollection and familiarity for single items but not scenes have been reported in a case of a rare PRC lesion with preserved hippocampus (see Lacot et al., 2017 for an extensive single-case study). However, it has been argued that these findings were not conclusive, because classic recognition paradigms use whole items at test, and thus subjects do not properly need to *complete* patterns. Hence, recollection and familiarity responses are not fully imputable to pattern completion and memory-strength signal operations, respectively. Ross, Sadil, Wilson, and Cowell (2018) used a well-designed functional magnetic resonance imaging (fMRI) study to overcome this issue. They used a Remember/Know (R/K) recognition paradigm in which participants are

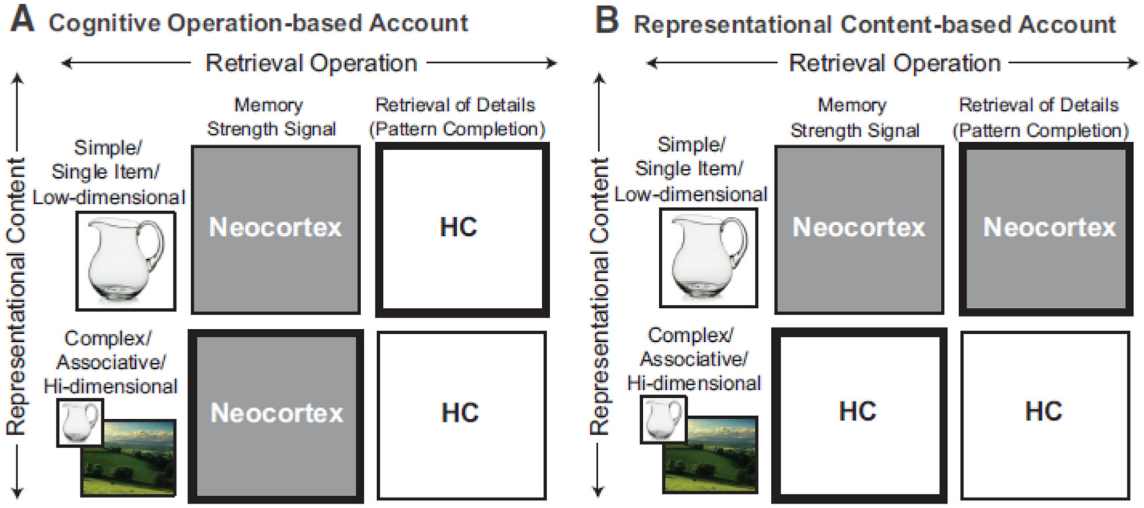

**Fig. 1 — Illustration from Cowell et al. (2019), adapted from Ross et al. (2018). A. Schematic illustration of the operation-based account. B. Schematic illustration of the representational-based account. HC: Hippocampus.**

instructed to judge items as old or new and to indicate for the recognised items whether they specifically *remember* seeing them before (i.e., recollection), or they simply *know* that they have seen them (i.e., familiarity). Yet, as mentioned above, such paradigms cannot properly elicit pattern completion, as the to-be-recalled items are presented on the screen at test, and therefore participants do not need to mentally *complete* them. To solve this issue, as the key feature of their apparatus, Ross et al. presented the stimuli in the form of visual patches (i.e., small circular windows) at test, displaying only limited portions of the stimuli instead of the whole stimuli. The participants thus responded with an R only when they could reconstruct the stimuli from memory, which can be interpreted as pattern completion. Stimuli dimensionality was manipulated, with half of the stimuli being objects (i.e., low-dimensionality condition) and the other half being scenes (i.e., high-dimensionality condition). In this way, Ross et al. were able to test the four conditions represented in the 2 × 2 matrix in Fig. 1. They reported hippocampal activation during the pattern completion of scenes but not of objects, which instead recruited the PRC.

Ross et al.' study strongly supports that the representational content of the memory retrieved, and not the type of retrieval operation, determines the brain structures involved during memory retrieval. However, this demonstration concerns only pattern completion. If MTL structures are specialised according to representations and not operations, then the pattern of results observed in this study should be found for other operations such as the generation of a memory-strength signal, or even visual perception. K responses reflect familiarity, or memory-strength signal recognition. Ross et al. reported no activation of the hippocampus associated with K responses for scenes. One interpretation of this result could be that the function of the hippocampus is, after all, recollection, which involves *both* the operation of pattern completion *and* a complex, associative memory content. However, given that recognition was performed on patch stimuli, participants judged only these visual patches as familiar, not the whole stimuli. Consequently, the representations processed in these trials were not scenes but parts of scenes, which cannot be regarded as high-dimensional representations. In other words, if these stimuli were complete, the hippocampus would have been recruited during K responses for scenes, according to the RH model.

The present study aims to assess this issue by replicating Ross et al.' protocol with a whole-item condition in addition to the patch-cue condition (Fig. 2). Therefore, we expect K responses for whole-item scenes to elicit hippocampal activations in comparison to whole-item objects. This prediction results from the hypothesis that the representation (i.e., scenes or objects), and not the operation (i.e., memory-strength-signal) determines the MTL structures involved in familiarity-based memory. Yet, whether the signal that is generated is strong enough to trigger familiarity judgement does not affect the dimensionality of the representational content of the cue stimulus. Therefore, whether a memory-strength-signal does trigger a familiarity judgement or not should not affect the MTL structures involved in this process, which should instead be recruited according to the dimensionality of the stimulus. In other words, correctly rejected high-dimensional stimuli should activate the hippocampus similarly to those stimuli leading to correct K responses. We hence expect new whole-item scene processing (i.e., correct rejections; Fig. 2) to recruit the hippocampus in comparison to new whole-item objects processing.

Furthermore, if the functional organisation of the ventral-visual stream and MTL structures is independent of operations, then non-mnemonic operations should elicit patterns of activation similar to mnemonic operations, according to the representations processed. This is one essential assumption of the RH view (Bussey & Saksida, 2007; Cowell et al., 2009; Saksida & Bussey, 2010). Evidence supporting this idea comes from studies that report visual-discrimination deficits for scenes only in patients with selective hippocampal lesions and for scenes and faces in patients with larger MTL lesions that include the PRC (Barense et al., 2007; Lee, Buckley, et al., 2005; Lee, Bussey, et al., 2005; Lee et al., 2012 for review). The reciprocal pattern of brain activations (i.e., hippocampus for scenes and PRC for faces and objects during visual processing)

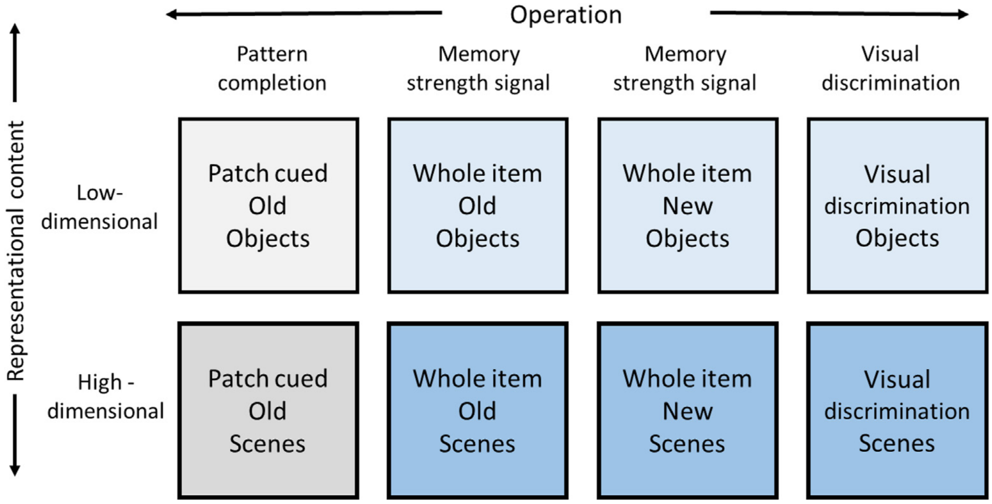

**Fig. 2 – Schematic illustration of the matrix taken from Ross et al. (2018) extended to additional operations. Grey boxes represent conditions investigated by Ross et al.; blue boxes represent conditions added in the present study.**

has been reported in fMRI studies (e.g., Barense et al., 2010; Hodgetts et al., 2017; Lee et al., 2008; McCormick et al., 2021; McCormick & Maguire, 2021; Zeidman et al., 2015). Notably, some studies suggest that presenting the stimuli from different viewpoints is crucial to demonstrate such results in visual-discrimination tasks (Barense et al., 2010; Lee, Buckley, et al., 2005; Lee et al., 2006; review in Graham et al., 2010). When contextualising these results in the representational view, visual discrimination can be considered an operation in the same way as pattern completion or memory strength signal. Therefore, we proposed to extend the results observed by Ross et al. to this non-mnemonic operation by using a visual-discrimination task during fMRI scanning, which constituted the encoding phase for the memory task, thus using the same stimuli in all investigated operations.

In summary, the present study aimed (1) to replicate the results from Ross et al. (2018) concerning hippocampal engagement during pattern completion; and to extend these results (2a) to other mnemonic operations (i.e., memory-strength recognition and rejection) and (2b) to a non-mnemonic operation (i.e., visual discrimination). To that end, we used an fMRI protocol based on the original paradigm with additional experimental conditions (Ross et al., 2018). Participants first performed a visual discrimination task with scenes and objects; they then performed an incidental R/K recognition task in which scenes and objects were presented in full to one group of participants and in the form of visual patches to the other group. Our main hypotheses were that the hippocampus would be activated by any operation (i.e., pattern completion, memory-strength signal recognition and rejection, and visual discrimination) for scenes but not objects.

## 2. Methods

### 2.1. *Power analysis*

To calculate the size required for an adequately powered sample, we used the software G*power. The main hypothesis of this project is the replication of the results by Ross et al. (2018; i.e., hippocampal engagement in pattern completion of scenes but not objects). Ross et al. conducted a regions of interest (ROIs)-based within-subjects Anova: $F_{1,19} = 6.61$. Using this statistic, we estimated an effect size of .589. Given that Ross et al. reported a $p$ value of $p = .019$, we chose to use a threshold of alpha = .02. The power analysis based on this effect size, for a power of .9 and an alpha = .02, for a within-subjects (2 × 2; Section 2.6.2.3.2) Anova, revealed a required sample size of n = 22.

We then conducted a literature search to select, for each preregistered hypothesis, fMRI studies that reported hippocampal activations as results of similar effects. We calculated post-hoc effect sizes for each selected study on the basis of reported statistics, or directly identified the effect size when reported. When several active clusters were reported in one hippocampal ROI, or different clusters in right and left hippocampi, the lowest statistical value was retained to estimate the effect size. We subsequently used these estimated effect sizes to calculate minimal the sample size required to achieve >90% power at alpha = .02 for each of our hypotheses.

The estimated effect size for the whole-item recognition of scenes versus objects hypothesis (Section 2.6.2.3.3) was .655 (Z = 3.49; Hassabis et al., 2007). The minimal required sample size calculated on the basis of this effect size was n = 20. The estimated effect size for the whole-item rejection of scenes versus objects (Section 2.6.2.3.3) was .606 (Z = 3.36; Rombouts et al., 2001). The minimal required sample size calculated on the basis of this effect size was n = 22.

The estimated effect sizes for the visual-discrimination of scenes versus objects hypothesis (Section 2.6.2.3.1) were .997 (Z = 5.86; Lee et al., 2008), .807 (Z = 3.96; Lawrence et al., 2020), .799 ($F_{2,44} = 14.14$; $\eta 2 = .39$; Hodgetts et al., 2017), .999 (Z = 6.34; Zeidman et al., 2015), and .694 (Z = 3.6; Barense et al., 2010). The largest minimal required sample size calculated on the basis of these effect sizes was n = 18. Finally, the estimated effect size for the scenes rotation effect hypothesis (Section 2.6.2.3.1) in visual discrimination was .728 (Z = 3.7; Barense et al., 2010). The minimal required sample size calculated on the basis of this effect size was n = 16.

Therefore, the minimal sample size required for the visual-discrimination task is n = 18, whereas the minimal sample size required for the recognition task is n = 22. Given that the recognition task was designed between-subjects (i.e., half of the participants were assigned to the whole-item condition whereas the other half were assigned to the patch-cue condition), and that the preregistered hypotheses for this task concern only one of these conditions, a minimum of 22 subjects was required per group. Our study therefore needed 50 participants overall, with 25 participants per group in the recognition task.

### 2.2. *Participants*

A total of fifty-nine healthy young adult participants were recruited through posters at the Grenoble-Alpes University campus (Grenoble, France). Two participants were excluded because of technical difficulties, and one due to excessive head motion during scanning. After applying exclusion rules for behavioural responses (see 6.1), 51 participants were included in the analyses of the visual-discrimination task, and 25 in each condition of the recognition task analyses. All participants were native French speakers, right-handed, and had normal or corrected vision. Mean age was 21.3 (standard deviation [SD] = 2.1; range 18–30; 13 males). Before taking part in the study, participants were screened for magnetic resonance imaging (MRI) safety and gave their informed consent. This study was governed by French law (Jardé, Décret n° 2016–1537; 16 November 2016) and the protocol has been approved by the National French Ethics Committee for the Protection of Human Subjects (CHUGA promotion; CPP 2020-A01592-37; ClinicalTrials ID NCT04562974).

#### 2.2.1. *Inclusion criteria*

- Normal or corrected visual acuity, allowing normal perception of the experimental material.
- Informed consent signed before taking part in the study.
- Age between 18 and 35 years.
- No contraindication to MRI scanning.
- Affiliated with the French social security system (healthcare system).

#### 2.2.2. *Exclusion criteria*

- Existence of a severe general health condition (e.g., heart or respiratory, haematologic, renal, hepatic, cancerous)
- Pharmacological treatment likely to modulate brain activity (e.g., benzodiazepines, antidepressants, neuroleptic, lithium)
- Diagnosed psychiatric or neurological condition (e.g., cerebrovascular accident, epilepsy)
- Alcohol ingestion before examination
- Claustrophobia
- People concerned by L1121-5 to L1121-8 of the French public health code (i.e., pregnant or breastfeeding women, subjects under 18 or over 18 years protected by the law, and subjects under administrative or legal surveillance).
- Uncorrected visual disorder
- Cognitive deficit (criterion: Mini-Mental Statement Examination score of <27)

### 2.3. *Procedure*

The experimental procedure began with a neuropsychological examination, including the Mini-Mental Statement Examination (Kalafat et al., 2003) and the Trail-Making Test, Part A and B (Lezak et al., 2004; Mitrushina et al., 2005). Participants then underwent a training session for the matching task. During the training phase only, feedbacks were given on the accuracy of each response; in the case of error, the stimuli remained on-screen until the participant pressed a key in order to ensure that they became familiar with the task. After checking that participants understood the instructions, they underwent the scanning session. The protocol was composed of two experimental tasks, both performed during MRI scanning. Stimuli were displayed with OpenSesame software (Mathôt et al., 2012) and projected onto a translucent screen (1366 × 768 pixels) at the rear of the MRI scanner, visible via a mirror placed on the head coil. Participants provided their responses manually.

#### 2.3.1. *Matching task*

2.3.1.1. TASK PROCEDURE. During the matching task, each trial was composed of three visual stimuli: one (i.e., the reference) positioned above the other two (i.e., the target and the lure; Fig. 3). Participants were given the instruction to determine which of the two images presented below matched (i.e., described the same stimulus as) the reference image. Each trial lasted 6 sec. After an answer was given by the participant, the lure and target images disappeared, but the reference image remained on-screen. Each reference stimulus was thus displayed for the same duration (i.e., 6 sec), hence controlling for encoding time. Two variables were manipulated: stimulus type[1] (scenes and objects), and spatial rotation (present, absent), resulting in four experimental conditions. There were 32 stimuli per condition (i.e., 128 trials overall). Trials were paired into 12-sec pseudo-blocks. The task was divided into two functional runs of 10 min, each including 32 task blocks and 6 rest blocks consisting in a fixation cross displayed for 12 sec. Blocks were separated by 4-sec inter-stimulus intervals, consisting of a grey fixation dot displayed on a black screen. Response accuracy and response time were recorded.

2.3.1.2. STIMULI AND MANIPULATIONS. Scene stimuli were images depicting realistic 3D scenes that include spatial landmarks (e.g., a square, a bedroom) and were built by using freely available software (https://unity.com). Object stimuli were images depicting realistic familiar 3D objects (e.g., a pan, a chair). Object images were built by using commercially available software (https://www.sketchup.com). Objects were positioned on grayscale noise backgrounds, randomly generated to reproduce the visual complexity (amplitude of the spatial-frequency power spectrum) and luminance of scene images, thus controlling these factors across conditions. All

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[1] The variable “stimulus type” was first termed stimulus “nature” in stage 1 manuscript. It was renamed following stage 2 review for clarity.

**Fig. 3 – Experimental design. Left: Examples of trial in the Matching task, in the object and scene conditions, with spatial rotation manipulation. Right: Example of visual patch and original scene image.**

images were grayscale 640 × 360 pixel images (the size of object backgrounds equalled that of scene images). All stimuli were emotionally neutral, and none included any shocking or sensitive content. Half of the trials included a spatial rotation, consisting in a 40- to 60-degree shift in point of view either to the right or to the left. In these trials, the point of view in the reference differed from that of the target and lure, which always displayed the same point of view. All images can be viewed in Supplementary material on the Open Science Framework (OSF) project page.[2]

### 2.3.2. *R/K recognition task*

2.3.2.1. Task procedure. During the recognition task, scenes and objects from the matching task were presented again to the participants, mixed with new stimuli of the same type. A trial was composed of one stimulus displayed in the centre of the screen for 6 sec. The task was divided into two runs of 64 trials (i.e., 128 trials overall), each including 24 old and 8 new scenes and 24 old and 8 new objects, as well as 32 baseline trials (i.e., null events), consisting in a fixation dot displayed for 4 sec. Events (i.e., scenes, objects, and null events) were presented in a pseudo-randomised order. Half of the participants (N = 25) underwent the whole-item condition, whereas the other half underwent the patch-cue condition. Participants were randomly assigned to one of the conditions. Participants were not given the instruction to try to remember stimuli during the first task, thus ensuring incidental encoding. Both groups of subjects were instructed to judge each stimulus as *old* or *new*, that is, to determine whether or not it had been presented during the previous task. When an answer was given, the image displayed disappeared and was replaced by the inter-stimulus fixation cross, thus informing the participant that their response had been recorded.

2.3.2.2. Instructions in the patch-cue condition. In the patch-cue condition, stimuli were presented in the form of visual patches. Participants had three response options: ‘1’ if they were able to visually reconstruct the original image from the patch (Rec responses); ‘2’ if the patch seemed familiar to them but they could not reconstruct the original image (K responses); and ‘3’ if they thought the patch had not been presented before (new responses).

2.3.2.3. Instructions in the whole-item condition. In the whole-item condition, stimuli were presented in the same form as during the matching task (i.e., entirely). Participants had three response options: ‘1’ if they specifically remembered seeing the stimulus during the first task (R responses); ‘2’ if the stimulus seemed familiar to them but they did not specifically remember seeing it before (K responses); and ‘3’ if they thought the stimulus had not been presented before (new responses).

2.3.2.4. Stimuli and manipulations. Two variables were manipulated: *stimulus type* (scenes and objects), and *clue type* (whole images *vs* patch clue). Sixty-four scenes and 64 objects were used in the recognition task, each composed of 48 old stimuli taken from the matching task and 16 new items. All images were presented in the centre of the screen in the same dimensions as during the matching task (640 × 360 pixels). In the whole-item condition, stimuli were presented entirely (i.e., whole-image condition), whereas in the patch-cue condition, only visual patches were displayed (Fig. 3). Visual patches consisted in 150-pixel-diameter circular images, taken at various positions from the original images and based on the same criteria as in the original study: patch positions were chosen to include enough elements to be recognisable, but to not include critical elements that would make recognition obvious (Ross et al., 2018).

2.3.2.5. Briefing and debriefing sessions. Remember/know paradigms are very powerful to investigate the nature of memory retrieval, by relying on participants' subjective feeling; it hence comes with a briefing and a debriefing session (Diana et al., 2006; Migo et al., 2012; Rajaram, 1993). First, we ensured that each participant had fully understood the R/K instructions before the task began. To do so, we provided

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[2] OSF link: https://osf.io/cbds5/?view_only=8dff7226148143c2b8a9a4a4efcfab01.

participants with examples of the subjective feeling associated with each type of response, and encouraged them to ask questions until they had a good comprehension of what each response option meant (i.e., *Rec vs K* in the patch-cue condition and *R vs K* in the whole-item condition; see Sections 3.2.2 and 3.2.3). They were explicitly told to respond according to their subjective feeling. At the end of the experiment, participants also underwent a debriefing session, in which we ensured that they responded according to R/K instructions. As was done in Ross et al. (2018), participants were aware that a debriefing session would take place at the end of the recognition task, thus encouraging them to respond as accurately as possible.

## 2.4. Behavioural pretests and task adjustment

The behavioural procedure and material were pretested among 12 healthy young participants. The pretest sample was recruited in order to match the anticipated test sample in terms of demographic criteria (i.e., students aged 18–35). Trial-by-trial correct response rates were extracted from the matching task to identify and remove stimuli that were too difficult (<60%) or too easy (>90%). Correct response rates were thus stabilised at around 75%–85% (see Barense et al., 2010; Lee et al., 2008, for similar designs in fMRI studies). Rates of correct responses were extracted from the recognition task, eliciting a correct response rate of 77% for old items and 84% for new items. Participants in both the whole-item condition (mean correct rate = 84.63%) and in the patch-cue condition (mean correct rate = 68.02%) demonstrated reasonable overall performance. Rates of R and K responses were extracted, showing on average of 41% R and 29% K responses for old patch-cue items, and 61% R and 20% K responses for old whole items.

## 2.5. MRI data acquisition and preprocessing

### 2.5.1. Scanning parameters

MRI and fMRI data were collected using a 3T scanner (Achieva dStream 3.0T TX, Philips Medical Systems, Best, NL) with a 32-channel head coil at the IRMaGe MRI facility (Grenoble, France). First, T1-weighted, high-resolution, 3D anatomical scans were acquired (field of view (FOV) = 256 × 192 × 220; resolution = 1 × 1 × 1 mm; acquisition matrix = 256 × 256 pixels, reconstruction matrix = 256 × 256 pixels). Functional data were then acquired using a BOLD-sensitive T2*-weighted echo-planar imaging (EPI) method. According to the hypotheses and in order to increase spatial resolution, a reduced FOV (100 × 240 × 60) was used, focused on ROIs (i.e., medial temporal areas). Each volume was composed of 40 slices, acquired sequentially in an ascendant mode. Slice thickness was 1.5 mm. The in-plane voxel size was 1.27 × 1.27 × 1.5 mm (166 × 160 pixels data matrix; 192 × 192 pixels reconstruction matrix). The main sequence parameters were: TR = 2 sec; TE = 30 msec; flip angle = 80°. One whole-brain EPI image was acquired for the coregistration preprocessing step.

### 2.5.2. Preprocessing

fMRI data were preprocessed with SPM 12 (SPM, Welcome Department of Imaging Neuroscience, London, U.K; www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks Inc., Sherborn, MA, USA). First, a realignment step was performed to correct for subtle head movements. Realigned functional images were then coregistered to the whole-brain image. A second coregistration step served to replace the anatomical image onto the whole-brain functional image. Finally, functional images were smoothed with a 3-mm Full Width at Half Maximum (FWHM) Gaussian kernel. Noise and signal drift were removed by using a high-pass filter (1/128 Hz cut-off). Preprocessed data were then statistically analysed.[3]

### 2.5.3. Exclusion rules for MRI data

Motion parameters from the realignment step were then analysed using ART (Artifact Detection Tool, Gabrieli Lab, Massachusetts Institute of Technology, available at: https://www.nitrc.org/projects/artifact_detect). Were considered as outliers those volumes that showed more than 1.5 mm interscan movement in translation, .02 rad in rotation, or 3 SD global interscan signal intensity relative to the session mean. Participants who had more than 15% of scans marked as outliers were excluded from the study (N = 1).

## 2.6. Planned analyses

### 2.6.1. Behavioural data

Behavioural data from the matching task included rates of correct responses (CRs) and errors (response times were not of interest to our purposes) for each participant for each run. The study being conducted among healthy young participants, we expected them to succeed in all conditions of the task. We expected the mean CR rate to be above 70% correct[4](Barense et al., 2010; Lee et al., 2008). To be included in the analyses, the rate of CRs for a participant had to be at least 70%, thus ensuring that participants performed the task properly.

Behavioural data from the recognition task included CR and error rates as well as rates of remember and know responses, for each participant for each run. Correct responses consisted in correct recognitions (R/rec or K for old items) and correct rejections (New for new items); errors consisted in false alarms (R/rec or K for new items) and omissions (New for old items). We expected the mean CR rate to be above 70% correct (Ross et al., 2018). To be included in the analyses, the rate of CRs of a participant had to be at least 70%, and rates of correct R/rec and K responses had to be of at least 20%, thus insuring that participants performed the task properly, and that all response types were represented.

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[3] As suggested during stage 1 review, we drew individual masks on each subjects' anatomical scan and extracted the parameter estimate using these masks. We therefore used native functional images, but forgot to remove the normalisation step from the Stage 1 manuscript in preprocessing; we thus removed this part from the stage 2 manuscript.

[4] In stage 1 we proposed to exclude participants who would not fall into the interval 70–90% correct; however, excluding a slightly too performant participant would make no sense, as long as the task was not too easy in general, which was not the case (Matching M = 82.6%, SD = 4.6; Recognition M = 83.03%, SD = 8.2). We therefore chose to keep the 70% correct minimal threshold to exclude participants.

### 2.6.2. *Statistical fMRI analyses*

This study was preregistered with the Open Science Framework, the original proposal can be found at: https://osf.io/stn9p.

2.6.2.1. Statistical design. Following preprocessing, statistical analyses were performed using the general linear model (GLM) as implemented in SPM12. (i) Matching-task runs were analysed as a block design, including 2 factors: stimulus type (i.e., scenes and objects) and rotation (i.e., rotation, no rotation). These 4 experimental conditions were modelled as a boxcar function of 12-sec duration (i.e., the duration of a pseudo-block) and convolved with the canonical haemodynamic response function to create regressors of interest. (ii) Recognition-task runs were analysed as an event-related design[5] including 2 factors: stimulus type (i.e., scenes, objects) and driven-subject correct response (i.e., R/Rec, K, and new). These 6 experimental conditions were convolved with the canonical haemodynamic response function to create regressors of interest. Movement parameters obtained by realignment corrections were included as noise (regressors of no interest).

2.6.2.2. Regions of interest (ROIs). Disclaimer: this section was rewritten due to ambiguities that emerged during stage 2 review. To prevent from any bias resulting from the ROI definition, a validation analysis was conducted (see Results – Exploratory analyses).

ROIs were defined on each individual's non-normalised structural brain image. The Automated Segmentation of Hippocampal Subfields approach (ASHS; Yushkevich et al., 2015) was first performed, then ROIs were manually edited by using MRIcron (https://www.nitrc.org/projects/mricron). The sub-regions of the parahippocampal gyrus (including Broadman areas 35 and 36) were combined into the parahippocampal region, and controlled following the principles described by Allen et al. (2005). This parahippocampal regions was then subdivided into three sections of equal length: an anterior segment corresponding to the perirhinal cortex, a posterior segment corresponding to the parahippocampal cortex, and a middle segment corresponding to the transition zone between these regions (Ross et al., 2018; for a similar approach, see also Hannula et al., 2013). Using the same approach, we divided the hippocampus longitudinally into three segments corresponding to the anterior, middle, and posterior hippocampus (Fig. 4). ROI drawings were checked by a researcher (MD) with extensive neuroanatomy experience, including that related to the hippocampus and MTL structures, and were adjusted where necessary in discussion with the research team. Parameter estimates were then extracted from these ROIs across the experimental conditions by using the Nilearn python module (https://nilearn.github.io/index.html). After verifying the homogeneity of variances, and removing extreme values, these parameter estimates were entered into specific within-subjects mixed regressions. Given that our main hypothesis is the replication of an effect reported at $p = .019$ (Ross et al., 2018), we used a significance threshold of alpha = .02.

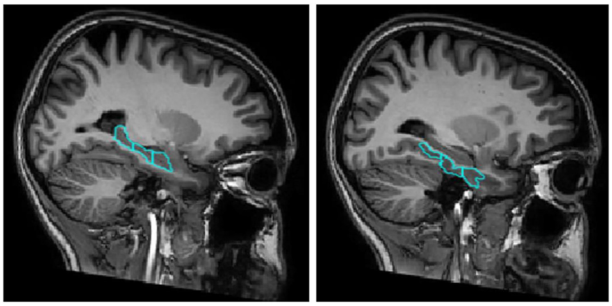

**Fig. 4 – Regions of interest drawn on one sample subject's anatomy. Left posterior, middle, and anterior hippocampus. Right: posterior, middle, and anterior (perirhinal cortex) parahippocampal gyrus.**

2.6.2.3. Hypotheses

2.6.2.3.1. Matching task. **Visual discrimination of scenes versus objects (H1):** The main hypothesis was that the hippocampus would be activated during the visual discrimination of scenes but not objects. Further, we expected the hippocampal engagement during visual perception to be increased by the presence of a spatial rotation. We thus expected to find a stimulus type × ROI interaction effect and a stimulus type × rotation interaction effect for the hippocampus only.

2.6.2.3.2. Recognition task – patch-cue condition. **Pattern completion of scenes versus objects (H2):** We aimed to replicate the finding observed by Ross et al. (2018): hippocampal engagement during pattern completion of scenes but not objects. The Rec responses (visual reconstruction in the patch-cue condition) for studied scenes (S-Rec) were compared with those for studied objects (O-Rec) across the hippocampus and PRC. We expected this analysis to reveal a stimulus type × ROI interaction effect.

2.6.2.3.3. Recognition task – whole-item condition. **Whole-item recognition of scenes versus objects (H3):** We first aimed to test whether hippocampal activations would be elicited by familiarity-based recognition (i.e., memory strength-signal) of whole-scene versus object images. The K responses (i.e., familiarity) for studied scenes were compared to those for studied objects across the hippocampus and PRC. Similar to hypothesis 2, we expected to observe a stimulus type × ROI interaction effect.

**Whole-item rejection of scenes versus objects (H4):** We then aimed to test whether correctly rejecting whole-scene images would recruit the hippocampus as compared with object images. New (N) responses for unstudied scenes were thus compared to those for unstudied objects across the hippocampus and PRC. We expected to find a stimulus type × ROI interaction effect similar to hypotheses 2 and 3.

2.6.2.3.4. Hippocampal ROIs analyses. **Pattern completion of scenes versus objects in the hippocampus long-axis ROIs (H5):** Ross et al. found evidence for a similar engagement of the

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[5] The recognition task was analysed as an event-related design because old and new stimuli in a recognition task must be presented in a random or pseudo-random order, thus preventing the use of block designs.

anterior, middle, and posterior hippocampus for pattern completion of scenes but not objects. We expected to replicate this result by observing a main effect of stimulus type only. Stimulus type simple effects would be explored if a stimulus type × ROIs interaction effect was observed.

## 3. Results

### 3.1. *Behavioural data*

Neuropsychological screening confirmed that all participants presented normal global cognitive functioning ($M_{MMSE} = 29.86$; $SD = .34$) and visuo-spatial abilities ($M_{TMT\ A} = 17.97$; $SD = 4.32$; $M_{TMT\ B} = 36.49$; $SD = 8.84$). Only participants who met the inclusion criteria were included for further analyses (cf. 6.1). Behavioural data confirmed that participants properly performed both the matching task ($M_{correct} = 82.64\%$, $SD = 4.62$) and the recognition task ($M_{correct} = 83.03\%$, $SD = 8.22$). Rates of R/K/N responses were comparable in the whole-item and patch-cue conditions (Whole-item: $M_R = 43.27\%$, $M_K = 32.15$, $M_{new} = 24.57$; Patch-cue: $M_R = 46.25\%$, $M_K = 33.15$, $M_{new} = 20.59$ of all correct responses).

### 3.2. *Imaging data*

#### 3.2.1. *Visual-discrimination task*

**Hypothesis 1**. As expected, we observed an ROI × stimulus type interaction during visual discrimination ($F_{1,195} = 131.74$; $p < .001$; Fig. 5). When decomposing this interaction, we found that the hippocampal activation was higher for scene than for object processing ($F_{1,49} = 42.89$, $p < .001$), whereas the PRC was more recruited by object than by scene processing ($F_{1,49} = 34.70$, $p < .001$). Contrary to our hypothesis, there was no stimulus type × Rotation interaction for the hippocampus ($p = .65$). In contrast, such an interaction was found in the PRC ($F_{1,48} = 9.43$, $p < .01$; Fig. 6). Simple effects revealed a significant effect of rotation for object processing ($F_{1,45} = 16.43$, $p < .001$), but not for scene processing ($p = .91$).

#### 3.2.2. *Patch-cue recognition task*

**Hypothesis 2**. As predicted, we observed a significant stimulus type × ROI interaction during pattern completion ($F_{1,22} = 26.64$; $p < .001$; Fig. 7). Consistent with the original study, the hippocampus was significantly more engaged during pattern completion of scenes than of objects ($F_{1,22} = 5.26$; $p < .05$). In contrast, the PRC was more engaged during pattern completion of objects than of scenes ($F_{1,22} = 8.65$; $p < .01$).

**Hypothesis 5**. Unlike Ross et al., we found no main effect of stimulus type when decomposing the hippocampus long axis ($p = .29$). Because we found a trend in the Long-axis segment × stimulus type interaction ($F_{1,47} = 4.89$; $p < .05$; Fig. 8), we explored by-segment simple effects. Whereas no effect of stimulus type was found in the posterior ($p = .173$) and middle ($p = .371$) segments, the anterior hippocampus showed greater engagement for pattern completion of scenes than of objects ($F_{1,22} = 4.77$; $p < .05$).

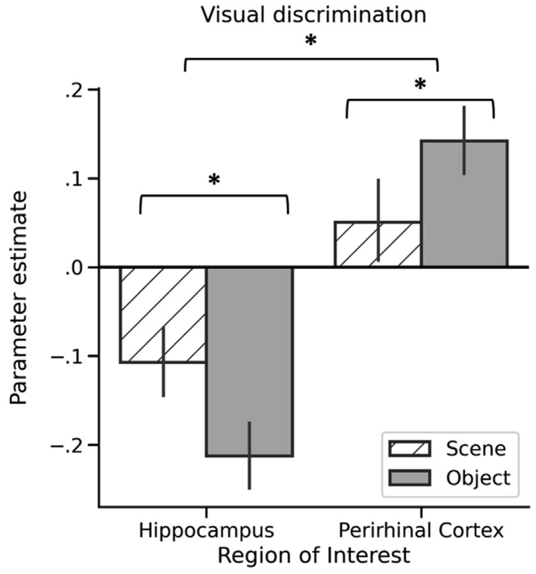

**Fig. 5 – Parameter estimate extracted in the matching task as function of regions of interest and stimulus type. Bar graphs represent means and 95% confidence interval.**

#### 3.2.3. *Whole-item recognition task*

**Hypothesis 3**. As expected, we observed an ROI × stimulus type interaction during correct familiarity-based responses ($F_{1,22} = 9.28$; $p < .01$; Fig. 9). Whereas hippocampal activity was

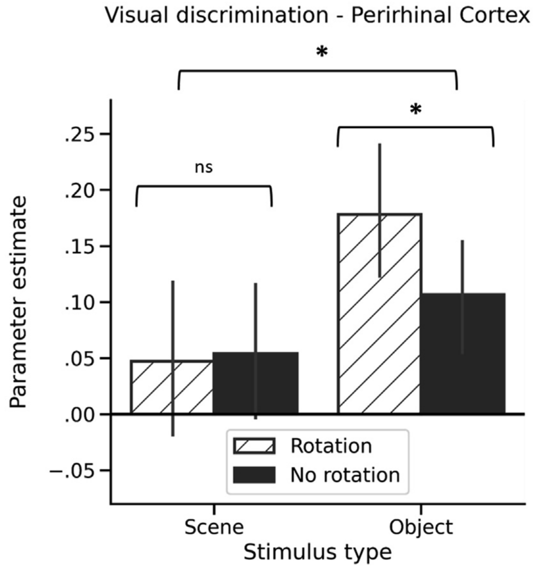

**Fig. 6 – Parameter estimate in the perirhinal cortex as function of stimulus type and rotation. Bar graphs represent means and 95% confidence interval.**

higher for scene than for object processing ($F_{1,22} = 4.53$; $p < .05$), the reverse pattern was found in the PRC ($F_{1,22} = 4.46$; $p < .05$).

**Hypothesis 4**. Consistent with our hypothesis, we found a stimulus type × ROI interaction during correct new responses ($F_{1,21} = 15.45$; $p < .001$; Fig. 10). The hippocampus was more activated by correct rejection of scenes than of objects ($F_{1,22} = 4.57$; $p < .05$), whereas no effect of stimulus type was found in the PRC ($p = .30$).

### 3.3. *Exploratory analyses*

#### 3.3.1. *Remember responses in the whole-item recognition task*

Our results accord with a broad/gist to sharp/detail model of the hippocampus anterior–posterior axis. This model makes another prediction: the posterior hippocampus should particularly respond to *recollection* as assessed by traditional R/K paradigms (i.e., the retrieval of details associated during encoding). We thus tested this hypothesis by analysing correct R responses in the whole-item recognition task, for scenes and objects, along the hippocampal long-axis. A main effect of segment was found ($F_{2,22} = 11.57$; $p < .001$, Fig. 11). Specifically, activity in the posterior hippocampus was stronger than in the middle ($F_{1,23} = 12.76$; $p < .01$) and stronger than in the anterior ($F_{1,23} = 21.75$; $p < .001$) segments. In contrast no difference was found between the anterior and middle segments ($p = .15$). Only a trend for main effect of stimulus type ($F_{1,23} = 5.49$; $p = .027$) as well as segment × stimulus type interaction ($F_{2,46} = 3.56$, $p = .036$) were found. Similar to the patch-cued condition, the effect of stimulus type (i.e., scene > object) was significant in the anterior ($F_{1,23} = 9.14$; $p < .01$) but not in the middle ($p = .073$) and posterior ($p = .84$) hippocampal segments. A trend for the reserve effect was observed in the PRC, with activity for object processing higher than for scene processing ($F_{1,24} = 5.32$; $p = .029$).

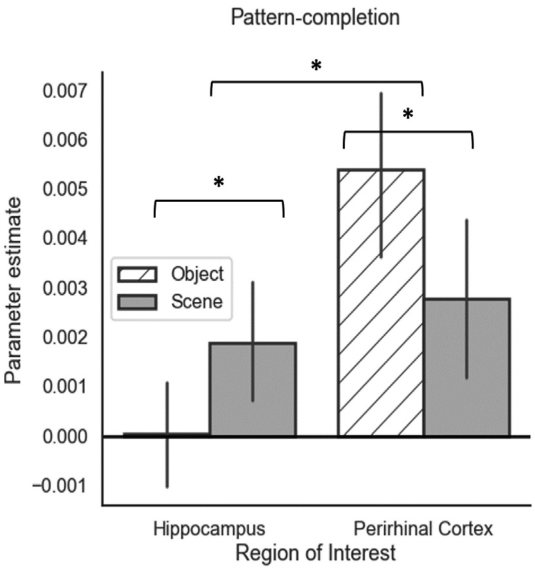

**Fig. 7 – Parameter estimate extracted in the patch-cue recognition task as function of regions of interest and stimuli stimulus type, for correct recall responses. Bar graphs represent means and 95% confidence interval.**

#### 3.3.2. *Further exploration of scene processing and spatial rotation effect in left versus right hippocampus long-axis segments*

Given that results in the matching task for scene stimuli were unexpected when analysing the hippocampus as a unique ROI, we explored the activity patterns across the hippocampus segments and hemispheres. We thus divided the hippocampus into 6 ROIs: left and right anterior, middle, and posterior segments; and tested the effect of the spatial rotation manipulation (i.e., different versus same presentation viewpoint) for scene processing. We found significant main effects of Hemisphere (i.e., stronger activity in the right than in the left hippocampus, $F_{1,42} = 23.46$; $p < .001$) and of Segment ($F_{1,41} = 6.63$; $p < .01$), as well as a Hemisphere × Segment interaction ($F_{2,297} = 5.11$; $p < .01$, Fig. 12). In the right hippocampus, activity was stronger in the middle than anterior segment ($F_{1,42} = 12.04$; $p < .01$) and stronger in the posterior than anterior segment ($F_{1,42} = 6.79$; $p < .02$), whereas no difference was found between the posterior and middle segments ($p = .95$). In the left hippocampus, no difference was found between activity in the middle and anterior segments ($p = .07$), whereas the posterior segment was more activated than in the middle ($F_{1,43} = 7.37$; $p < .01$) and anterior segments ($F_{1,42} = 13.8$; $p < .001$). We also observed trend for Hemisphere × Segment × Rotation interaction ($F_{2,296} = 3.92$; $p = .02$). A Segment × Rotation interaction effect was observed in the right ($F_{2,\ 83} = 7.13$; $p < .01$) but not in the left hippocampus ($p = .05$). Unexpectedly, activity in the right posterior hippocampus was decreased in presence of a spatial rotation as compared to the no-rotation condition ($F_{1,42} = 9.35$; $p < .01$). No effect of spatial rotation was found in the middle ($p = .88$) and anterior ($p = .33$) segments of the right hippocampus.

#### 3.3.3. *ROI definition validation analysis*

Because our definition of the PRC ROI slightly differed from that of the original study, we explore whether the results were influenced by this discrepancy. In particular, the PRC extends more anteriorly in the anatomical definition used by Ross et al. (Pruessner et al., 2000, 2002) than in the segmentation provided by ASHS (Yushkevich et al., 2015). All scans were segmented again on the basis of the former criteria. Parameter estimates from the matching task (N = 51) were extracted from those new PRC masks. We found very strong correlations between the signal extracted from these masks and the signal extracted from the initial masks, in all task conditions (all $r > .975$; all $p$-values $< .001$).

## 4. Discussion

### 4.1. *Replication of Ross et al. (2018)*

In the current study, we aimed at replicating the results observed by Ross et al. (2018)—that is, representational content determined MTL activity during pattern completion—and to assess whether it could be generalised to additional operations. To this end, we reproduced the original paradigm:

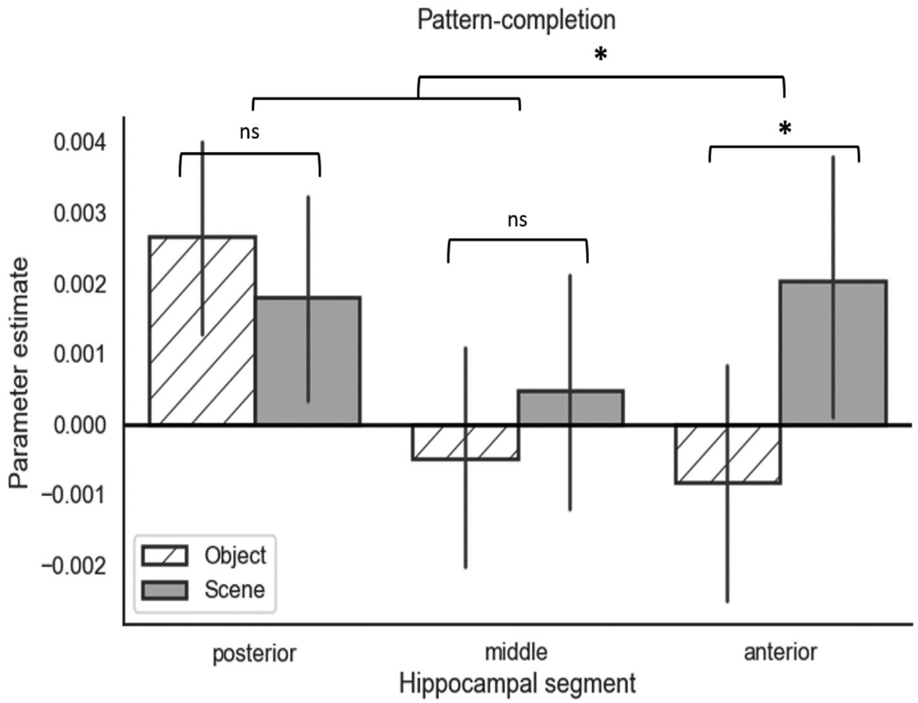

**Fig. 8** – **Parameter estimate extracted in the patch-cue recognition task as function of hippocampal long-axis segments and stimulus type for correct recall responses. Bar graphs represent means and 95% confidence interval.**

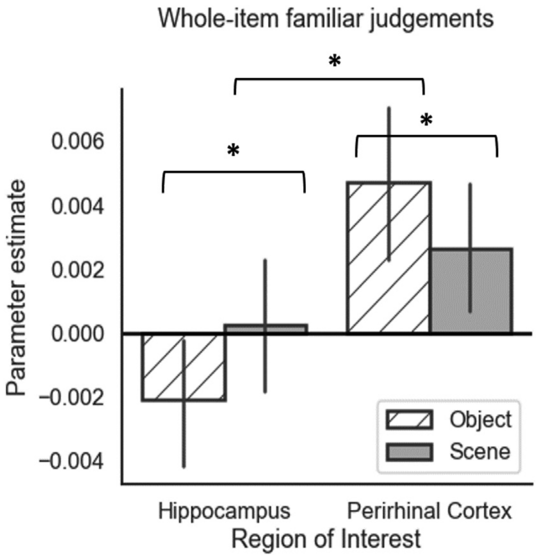

**Fig. 9** – **Parameter estimate extracted from the whole-item recognition task as function of regions of interest and stimulus type for correct *familiar* responses. Bar graphs represent means and 95% confidence interval.**

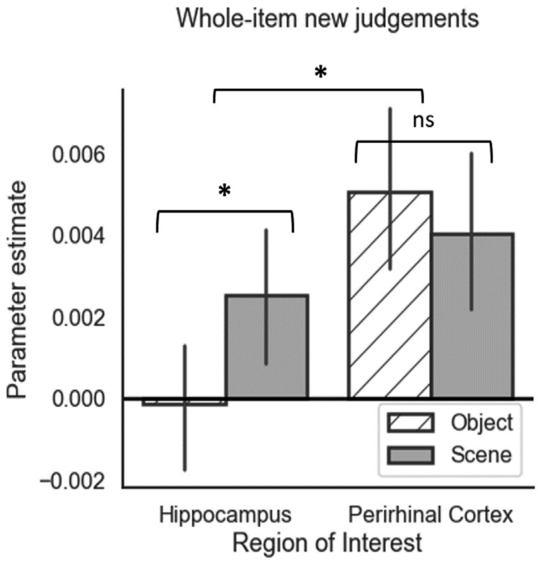

**Fig. 10** – **Parameter estimate extracted from the whole-item recognition task as function of regions of interest and stimulus type for correct new responses. Bar graphs represent means and 95% confidence interval.**

visual patches were used as memory cues in a recognition task. This apparatus allowed us to isolate the operation of pattern completion (i.e., *Rec* responses) while manipulating representational dimensionality. As expected, the hippocampus and PRC responded differently to scenes versus objects. In particular, the hippocampus was activated during pattern completion of scenes but not of objects. This preregistered replication strengthens the original demonstration that the contribution of the hippocampus to memory recall is determined by representational complexity rather than by the retrieval process. Contrary to the original findings, we also reported that the PRC was more activated by pattern completion of objects than of scenes. This is consistent with the representational hypothesis, in which it is expected that pattern completion is not limited to the hippocampus. Rather, this operation could happen at any stage of the ventral visual

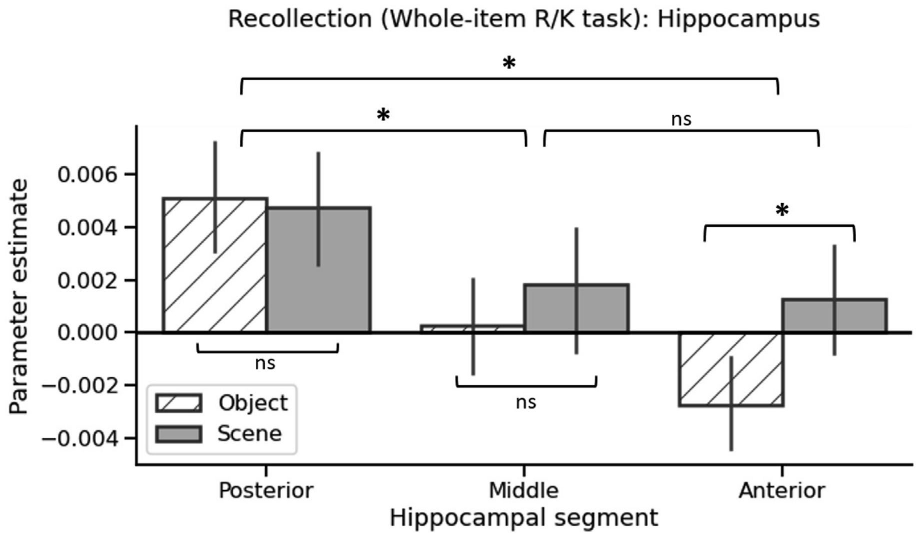

**Fig. 11 – Exploratory analysis 1: parameter estimate extracted from the whole-item recognition task as function of hippocampus long-axis segments and stimulus type for correct remember responses. Bar graphs represent means and 95% confidence interval.**

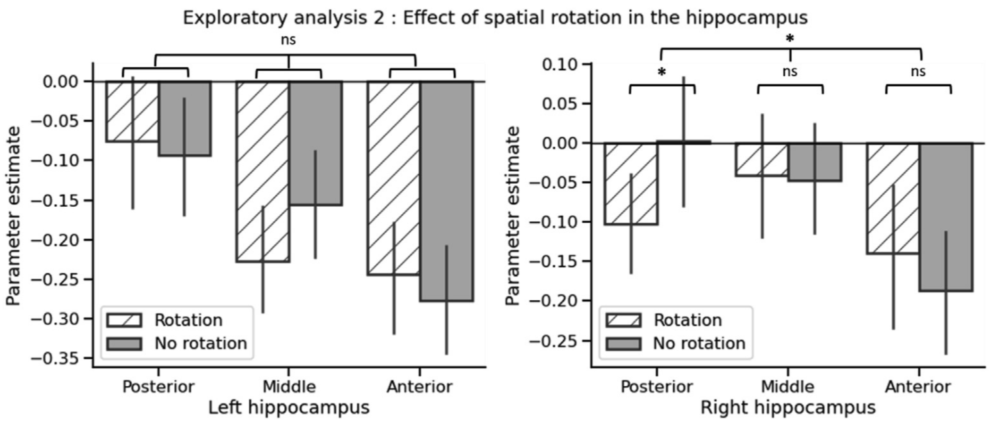

**Fig. 12 – Exploratory analysis 2: parameter estimate extracted in the matching task in the left and right hippocampus as function of hippocampal long-axis segments and spatial rotation manipulation. Bar graphs represent means and 95% confidence interval. Only simple effects of spatial rotation and rotation × segment interaction effects are represented; see main text for full details of statistical results.**

stream, depending on the dimensionality of the memory content, and the observed involvement of the hippocampus in processes such as recollection would reflect its specialisation in scene processing (e.g., Barense et al., 2005; Maguire & Mullally, 2013; Mullally & Maguire, 2014; Zeidman et al., 2015). We assume that differences in the content of the scene images could explain the discrepancy between the activity pattern that we observed in the PRC and that reported in the original study. Ross et al. used natural pictures of scenes that included objects and hence were more likely to rely on the PRC during recall. In comparison, the scene images that we used were refined to suit the visual-discrimination task, and thus contained minimal object features. Our study also differed regarding the type of task during encoding. Whereas in the original study, participants first completed a categorisation task, encoding in the present study consisted in a complex visual-discrimination task. This task requires in-depth visual processing of the images, and may arguably have enhanced the formation of internal representations of the objects. Thus, reconstructing these representations falls precisely into the scope of the PRC, that is, representing entities (Barense et al., 2010; Bastin et al., 2019; Besson et al., 2020; Cowell, 2012; Lacot et al., 2017). Overall, this pattern of results supports the representational hypothesis: the contribution of MTL regions to recall is determined by the dimensionality of the representation retrieved (Fig. 1B).

### 4.2. *Generalisation to other mnemonic operations*

We next investigated whether this pattern of results could be extended to operations other than pattern completion (Fig. 2). The representational account makes a clear prediction: this result should be generalisable to any operation, as long as the representations are held constant (Cowell et al., 2019). We first explored familiarity-based memory, or strength-signal recognition and rejection. Because “familiar” and “new” judgements made on visual patches cannot properly elicit such operations, we used a whole-item R/K paradigm to test this hypothesis. As predicted, MTL activity for whole-item familiar responses was modulated by representational content. Yet, whereas the object specialisation observed in the PRC was similar between strength-signal recognition and pattern completion, the scene specialisation of the hippocampus in strength-signal recognition was weaker than that found in pattern completion. One possible explanation for this discrepancy is that the hippocampus would be required when a scene representation needs to be *constructed* (Hassabis et al., 2007; Maguire & Mullally, 2013; Mullally & Maguire, 2014) or *reconstructed* as in pattern completion, but not in strength-signal memory. Yet, patients with hippocampal lesions elicit stimulus-dependent deficits in both familiarity and recollection memory (Bird et al., 2007; Cipolotti et al., 2006). Wais et al. (2010) also reported hippocampal involvement in familiarity-based recognition memory in fMRI. Notably, the authors controlled for memory strength confound by using confidence ratings, and argued that previous studies may have failed in demonstrating hippocampal activations in familiarity-based recognition because the memories associated with familiarity responses were too weak to generate a signal measurable with fMRI. It is possible that memory strength was confounded with remember-versus-familiar responses in the present study. Controlling for confidence rating in familiarity-based recognition memory while manipulating representational dimensionality may constitute an interesting lead for future research. An additional argument is the results observed for strength-signal rejection: the hippocampus was more activated for scenes than for objects, whereas the pattern was reversed for the PRC, albeit it was not statistically significant. Crucially, this demonstrates that the representational specialisation also applies to memory-strength rejection and hence is not limited to the operation of pattern completion. Overall, the results observed in the whole-item recognition task support the representational account, but call for further research to ascertain the scene specialisation of the contribution of the hippocampus to strength-signal recognition.

### 4.3. *Generalisation to visual-discrimination*

To further extend this effect to a non-mnemonic operation while using the same stimuli across all operations investigated, we used a visual-matching task as the encoding phase for later recognition. In line with the representational hypothesis, we expected to observe the same results as for pattern completion. In addition, because some studies reported that MTL engagement in visual processes is sensitive to viewpoint manipulations (review in Graham et al., 2010), we sought to test whether this manipulation was mandatory to show representational specialisation during a visual-perception task. Again, our findings were consistent with the representational hypothesis: the hippocampus responded preferentially to scenes as compared with objects, and the reverse effect was observed in the PRC. The spatial rotation effect was restricted to the PRC in our study with no significant effect in the hippocampus when analysed as a unitary ROI. Perirhinal activity during object processing, but not during scene processing, was enhanced by spatial rotation (i.e., different *vs* same viewpoints). These findings might seem to diverge from that of previous studies (Barense et al., 2010; see also Lee & Rudebeck, 2010). However, the effects for scene discrimination in those studies were found in the right posterior hippocampus specifically. We therefore conducted an exploratory analysis, and found that scene discrimination preferentially engaged the right as compared to left hippocampus, and particularly the right posterior hippocampus. Similar to Barense et al. (2010), the spatial rotation modulated activity in the right posterior hippocampus specifically; unexpectedly, however, this effect was the reverse of the original effect (i.e., viewpoint manipulation decreased instead of increased activity in this region). Although this analysis was unplanned and must therefore be interpreted with caution, this result is surprising. It might be explained by methodological differences between the two studies (e.g., matching versus oddity paradigm, task difficulty), and calls for further investigation of how the right posterior hippocampus contributes to spatial scene perception (see Zeidman et al., 2015). Overall, the pattern of results in the visual-discrimination task is consistent with those of previous studies reporting representation-specific MTL activity in non-mnemonic tasks (Barense et al., 2010; Hodgetts et al., 2017; Lee et al., 2008; McCormick et al., 2021; McCormick & Maguire, 2021; Zeidman et al., 2015), and confirm that this effect can be extended from mnemonic to non-mnemonic tasks even without spatial manipulation.

### 4.4. *Exploration of pattern completion in the hippocampus long-axis*

Ross et al. explored the hippocampus long-axis and reported evidence for representational specialisation of pattern completion in its anterior, middle, and posterior segments. We thus sought to replicate this result by dividing the hippocampus into three equal-length segments. Unlike in the original study, we found the anterior segment only to be preferentially engaged for scenes as compared with objects. Our results are consistent with a body a work showing a specific role of the anterior hippocampus in scene processing (Dalton et al., 2018; Hodgetts et al., 2017; McCormick & Maguire, 2021; Zeidman et al., 2015; Zeidman & Maguire, 2016). In particular, our results are in line with the proposal by Poppenk et al. (2013) that while the whole hippocampus contributes to pattern completion, the contribution of its anterior, but not middle and posterior portions, is specific to scene representations. According to this model, the anterior hippocampus would represent broad, gist information (including global spatial representations), whereas its posterior part would represent sharp, detailed information (including local spatial representations). Therefore, both the anterior and posterior hippocampus would be involved in pattern completion depending on the sharpness of the representation processed, which again is consistent with our results, as overall activity in these two segments during pattern completion was similar. In this view, scene construction and reconstruction fall into the scope of the anterior hippocampus. To unravel this effect, isolating the operation of pattern completion while manipulating the representation to complete is crucial, and was allowed by the use of the patch-cue paradigm. In contrast, *remember* responses in traditional R/K paradigms, which are attributed to proper recollection, usually reflect the presence of specific details associated with an item and retrieved during recognition (e.g., Migo et al., 2012; Montaldi & Mayes, 2010) and therefore rely more on the posterior hippocampus (Poppenk & Moscovitch, 2011). In an exploratory analysis, we consistently observed a linear posterior > middle/anterior segment effect for *remember* responses in the whole-item R/K task, regardless of representational content. Taken together, these results argue in favour of a hippocampal long-axis functional specialisation according to representation sharpness. Exploring the effect of representational content along the hippocampal long-axis provides a finer-grained extension of the RH account: whereas the use of scene versus object stimuli allows for evidence of hippocampus versus extra-hippocampal cortex specialisation, it may prove to be limited when investigating its internal functional organisation. In other words, the hippocampus processes different types of high-dimensional representations, and these different representations do not rely on the same hippocampal segments.

In summary, our findings support that the hippocampus is preferentially engaged in pattern completion, strength-signal memory, and visual discrimination, of scene stimuli as compared with objects, whereas the PRC is more involved in object processing across the same operations. By replicating the original result, and extending it to additional operations, our study supports the RH account: MTL activity is determined by representational content across operations (Bussey & Saksida, 2007; Cowell et al., 2019; Graham et al., 2010; Saksida & Bussey, 2010). Furthermore, representational specialisation in pattern completion was limited to the anterior part of the hippocampus, consistent with a broad-gist to sharp-details account of the hippocampal anteroposterior axis (Poppenk et al., 2013). These findings help bridge the gap between the RH model of the MTL and recent accounts of the internal functions of the hippocampus. Finally, the activation patterns observed in the middle segment of the hippocampus differed from those found in the posterior segment. While it is important to bear in mind that this study was not designed to dissociate between these two conceptions, this observation may support a three-segments rather than a two-segments fractionation of the hippocampal long-axis, and calls for further investigation of this issue (Strange et al., 2014).

## Credit author statement

Jeremy Gardette: Conceptualisation; Investigation; Writing – Original Draft.
Emilie Cousin: Methodology; Formal analysis.
Jessica Bourgin: Data Curation; Software.
Laurent Torlay: Methodology; Software.
Cédric Pichat: Methodology; Data Curation.
Olivier Moreaud: Resources; Project administration.
Pascal Hot: Conceptualisation; Writing – Review & Editing; Supervision.

## Open practices

The study in this article earned Open Data, Open Materials and Preregistered badges for transparent practices. Materials and data for the study are available at https://osf.io/3869n/?view_only=2eaedc798b6c4820ad3db0ac69e916d0.

## Conflict of interest

The authors declare that no conflict of interest exists.

## Data availability

Data will be made available on request.

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