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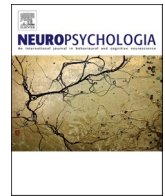
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# Proximity to boundaries reveals spatial context representation in human hippocampal CA1

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## ABSTRACT

Recollection of real-world events is often accompanied by a sense of being in the place where the event transpired. Convergent evidence suggests the hippocampus plays a key role in supporting episodic memory by associating information with the time and place it was originally encountered. This representation is reinstated during memory retrieval. However, little is known about the roles of different subfields of the human hippocampus in this process. Research in humans and non-human animal models has suggested that spatial environmental boundaries have a powerful influence on spatial and episodic memory, as well as hippocampal representations of contexts and events. Here, we used high-resolution fMRI to investigate how boundaries influence hippocampal activity patterns during the recollection of objects encountered in different spatial contexts. During the encoding phase, participants viewed objects once in a naturalistic virtual reality task in which they passively explored two rooms in one of two houses. Following the encoding phase, participants were scanned while they recollected items in the absence of any spatial contextual information. Our behavioral results demonstrated that spatial context memory was enhanced for objects encountered near a boundary. Activity patterns in CA1 carried information about the spatial context associated with each of these boundary items. Exploratory analyses revealed that recollection performance was correlated with the fidelity of retrieved spatial context representations in anterior parahippocampal cortex and subiculum. Our results highlight the privileged role of boundaries in CA1 and suggest more generally a close relationship between memory for spatial contexts and representations in the hippocampus and parahippocampal region.

## 1. Introduction

Episodic memory, the ability to remember past events, is intertwined with the place and time (spatiotemporal context) in which an event unfolded. Indeed, [Tulving \(1972\)](#) argued that the memory of an event is organized with respect to its spatiotemporal relation to other events. [O'Keefe and Nadel \(1978\)](#) built on this idea, stating that a specific brain area, the hippocampus, supports memory for items or events within a spatiotemporal context. Consistent with these general ideas, behavioral research has shown that spatial and temporal context reinstatement can influence episodic memory retrieval ([Eichenbaum, 2017](#); [Smith and Vela, 2001](#)), and neuroscience research has suggested that putative hippocampal representations for spatial ([Chadwick et al., 2011](#); [Deuker et al., 2016](#); [Kyle et al., 2015](#); [Miller et al., 2013](#); [Nielson et al., 2015](#);

[Rosenbaum et al., 2004](#); [Viskontas et al., 2009](#); [Zeidman and Maguire, 2016](#)) or temporal context ([Dimsdale-Zucker et al., 2018](#); [DuBrow and Davachi, 2016](#); [Eichenbaum et al., 2007](#); [Molitor et al., 2021](#)) are reinstated during episodic memory retrieval.

Mental representations of spatial context are structured by boundaries ([Epstein et al., 2017](#)). Research in animal models and humans alike has pointed to a privileged representation of spatial boundaries in neural activity, as they play a crucial part in models of navigation ([Epstein et al., 2017](#); [Julian et al., 2018](#)). For example, electrophysiological recordings in rodents have identified single cells in the entorhinal cortex and the subiculum that signal location and distance from borders in explored environments ([Barry et al., 2006](#); [Lever et al., 2009](#); [Savelli et al., 2008](#); [Solstad et al., 2008](#)) and neuronal oscillations in the medial temporal lobe of walking humans were shown to encode proximity to

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walls (Stangl et al., 2021). Consistent with these findings, hippocampal activity in humans during scene imagination relates to the number of boundaries in the environment (Bird et al., 2010), hippocampal activity during navigation in a virtual-reality task predicts learning of object locations relative to boundaries (Doeller et al., 2008).

Converging evidence points to the importance of non-spatial boundaries, moments in time identified by observers as a transition between events, for parsing continuous experiences (Kurby and Zacks, 2008). These transitions have been suggested to have a key role in organizing information in memory, and multiple studies have demonstrated the sensitivity and specificity of hippocampal responses to event boundaries (Baldassano et al., 2017; Ben-Yakov and Henson, 2018; Cohn-Sheehy et al., 2021; Reagh et al., 2020; Yoo et al., 2022; Zheng et al., 2022).

Here, we used a virtual reality exploration task paired with high-resolution fMRI to investigate how boundaries are reflected in the neural activity of the hippocampus and the extended episodic memory network (Maguire et al., 1998), consistent with the idea that the hippocampus binds information about space and time to create a unified representation of an experienced event (Eichenbaum et al., 2007; O'Keefe and Nadel, 1978) and that this representation is reinstated during memory retrieval.

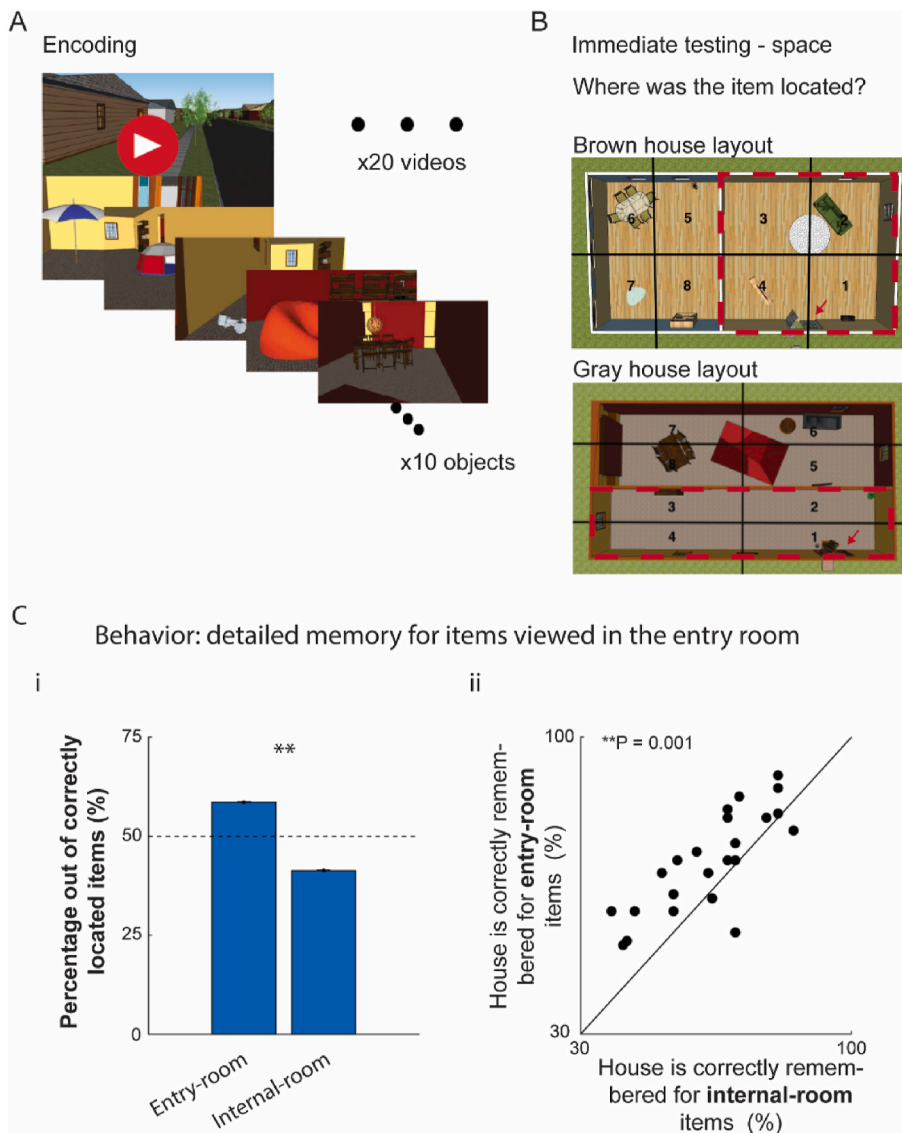
The hippocampus is composed of multiple interconnected subfields that contribute to memory processing and representation (Amaral and Lavenex, 2007). Characterizing their roles and interplay is essential for understanding how the hippocampus encodes context representations, which are the building blocks of complex episodic memories (Eichenbaum et al., 2007; O'Keefe and Nadel, 1978). Computational models propose that the unique anatomical properties of dentate gyrus (DG) and CA3 make these subfields ideal for *pattern separation*, the orthogonalization of highly similar inputs through sparse firing, whereas extensive connections from CA3 to CA1 via Schaffer collaterals, enable the reconstruction of memories from incomplete cues in CA1 and subiculum, also known as *pattern completion* (Guzowski et al., 2004; Marr, 1971; Norman and O'Reilly, 2003; Schapiro et al., 2017; Treves and Rolls, 1994; Yassa and Stark, 2011; Y. Zheng et al., 2021). It is unclear, however, whether these concepts capture the functional differences between subfields of the human hippocampus.

One method that has been used to uncover differences between hippocampal subfield representations is to compare their activity based on high-resolution functional magnetic resonance brain imaging (fMRI) measurement while subjects are asked to identify previously memorized visual stimuli and reject highly similar lures (Bakker et al., 2008; Berron et al., 2016; Lacy et al., 2010; Stevenson et al., 2020). Brain activity in these studies has been interpreted to reflect a bias towards pattern completion in CA1 and a tendency for pattern separation in CA3/DG. Can these results, based on unique visual stimuli, be extended to the prediction of how hippocampal subfields code for spatial context? In a study by Kyle et al (2015), virtual environments were used to test context-specific encoding in hippocampal subfields. Participants were first acquainted with four spatial contexts in a virtual environment and were later asked to estimate spatial distance between locations based on their acquired spatial knowledge. Comparing multivariate response patterns during these judgments demonstrated unique activation (remapping of representations) between spatial contexts in CA3/DG and less so in CA1. Pattern separation in CA2/CA3/DG (CA23DG) of different spatial contexts was also demonstrated by L. Zheng et al (2021), while others reported increased overlap in CA3 for similar environments (Stokes et al., 2015) and reduced overlap in CA1 (L. Zheng et al., 2021). These conflicting results point to the need for a deeper understanding of the interplay between subfields in the hippocampal circuit with respect to space. To our knowledge, no previous high-resolution fMRI studies have reported incidental reinstatement of spatial context information in particular hippocampal subfields during episodic recollection (without explicit retrieval of spatial information during scans).

In the present study, we revisited the data from Dimsdale-Zucker et al. (2018), (OSF | [abcdcon\\_pub](https://osf.io/abcdcon_pub)), to gain further insight into the nature of spatial context representation in the hippocampus in a virtual-reality paradigm that mimics the natural exploration of spatial environments. Participants viewed a set of videos, containing objects residing in two different spatial contexts (two houses), and they were scanned while they recollected these objects in isolation, devoid of any contextual information (Fig. 1A–B). Using high-resolution fMRI, we previously found that hippocampal subfields CA1 and a combined CA2/CA3/DG (CA23DG) play complementary roles in supporting the retrieval of episodic context (each video representing a unique episode) (Dimsdale-Zucker et al., 2018). In our previous study, we compared hippocampal activity pattern similarity (PS) for pairs of objects encountered in the same house (i.e., same spatial context) against PS for pairs of objects that were encountered in different houses (i.e., different spatial context). Initial analyses revealed no significant effects of spatial context in any hippocampal subfields or even in extrahippocampal regions such as the parahippocampal cortex (PHC) that are thought to support spatial context representation (Bastin et al., 2013; Brown et al., 2010; Deuker et al., 2016; Eichenbaum et al., 2007; Kunz et al., 2021; Morgan et al., 2011). This null finding was somewhat surprising given that participants were able to recall spatial contextual information about many of the studied objects.

In our re-analyses, we considered several possibilities: First, we investigated whether spatial context representation in hippocampal subfields might be tied to the successful encoding of the spatial context. We therefore examined pattern similarity (PS) during retrieval specifically for objects that subjects correctly associated with the specific room in which objects were encountered during encoding. Second, we considered whether the hippocampus might particularly carry information about objects viewed in the entry room of each house. These objects might be especially significant, given evidence for enhanced hippocampal encoding during event boundaries (Ben-Yakov and Henson, 2018; Cohn-Sheehy et al., 2021; DuBrow and Davachi, 2016; Reagh et al., 2020; Swallow et al., 2011) and hippocampal sensitivity to spatial boundaries (Bird et al., 2010; Julian et al., 2018; 2018b; Lever et al., 2009; Stangl et al., 2021). In our experimental paradigm, objects encountered in the entry room were both in proximity to the event boundary (start and end of the virtual tour) and near the boundary of the spatial context (entry point of the house). These considerations, as well as behavioral data in our study, suggesting that subjects generate a more detailed memory of these objects, led us to hypothesize the hippocampus would reflect a dedicated code for these entry room items.

We also considered the possibility that areas in the navigation network (Maguire et al., 1998) outside of the traditional hippocampal circuit might carry information about the spatial context. We focus here on the subiculum and the parahippocampal cortex (PHC) (Aggleton et al., 2010; Epstein, 2008; Kravitz et al., 2011; Ranganath and Ritchey, 2012) that encode information about spatial (Bastin et al., 2013; Brown et al., 2010; Deuker et al., 2016; Eichenbaum et al., 2007; Kunz et al., 2021; Morgan et al., 2011) and temporal context that is reinstated during recollection (Diana et al., 2013; Düzel et al., 2003; Essoe et al., 2022; Khader et al., 2005; Rugg and Vilberg, 2013). Recollection-related activity in PHC has been interpreted as having a central role in the representation of contextual information (Diana et al., 2013; Rugg and Vilberg, 2013). Subiculum, an output structure of the hippocampal circuit (Amaral and Lavenex, 2007; Ding, 2013), has also been linked to memory for spatial context (Lever et al., 2009; Peer et al., 2019; Zeidman et al., 2015; Zeidman and Maguire, 2016). Both the PHC and subiculum have been demonstrated to be reliably recruited during virtual spatial navigation in humans (Brown et al., 2010; Spreng et al., 2009; Zeidman et al., 2015). We hypothesized that better recollection performance would predict a more detailed memory for objects seen during the encoding phase, and tested for relationships between spatial context representations and individual differences in memory accuracy in these regions. We report here how spatial context, which is incidental to the



**Fig. 1. Revealing spatial context in a virtual-reality paradigm. (A-B) Experimental design. (A)** Participants encoded objects uniquely located within one of two houses (spatial contexts) across a series of 20 videos (episodic context). Each video was seen once (one-shot learning). **(B)** At the end of each video, participants were asked to place the encoded objects on a bird's eye map. Note that the two spatial contexts differed by their aspect ratio. The magenta arrows mark the entry doors' locations and the magenta dashed line marks the entry room of each house. **(C) Behavior:** (i) Encoding of objects viewed in the entry room was significantly better than that of objects encountered in the internal room: Each bar depicts the average number of successfully-placed images from each room, which is expected to be 50% if room identity does not affect memory; (ii) In a spatial memory test, taken after scanning, subjects were significantly better in recalling the house an object was viewed in for entry-room objects. Each dot represents one subject, y-axis represents the percentage of correct house choices for entry-room objects and x-axis is for internal room objects. (\*\* denote  $P < 0.01$ , using a paired, two-sided Wilcoxon rank-sum test).

recollection task, is reflected in hippocampus, subiculum, and PHC brain activity during successful recollection.

## 2. Results

### 2.1. Behavioral results – enhanced source memory for objects in the entry room

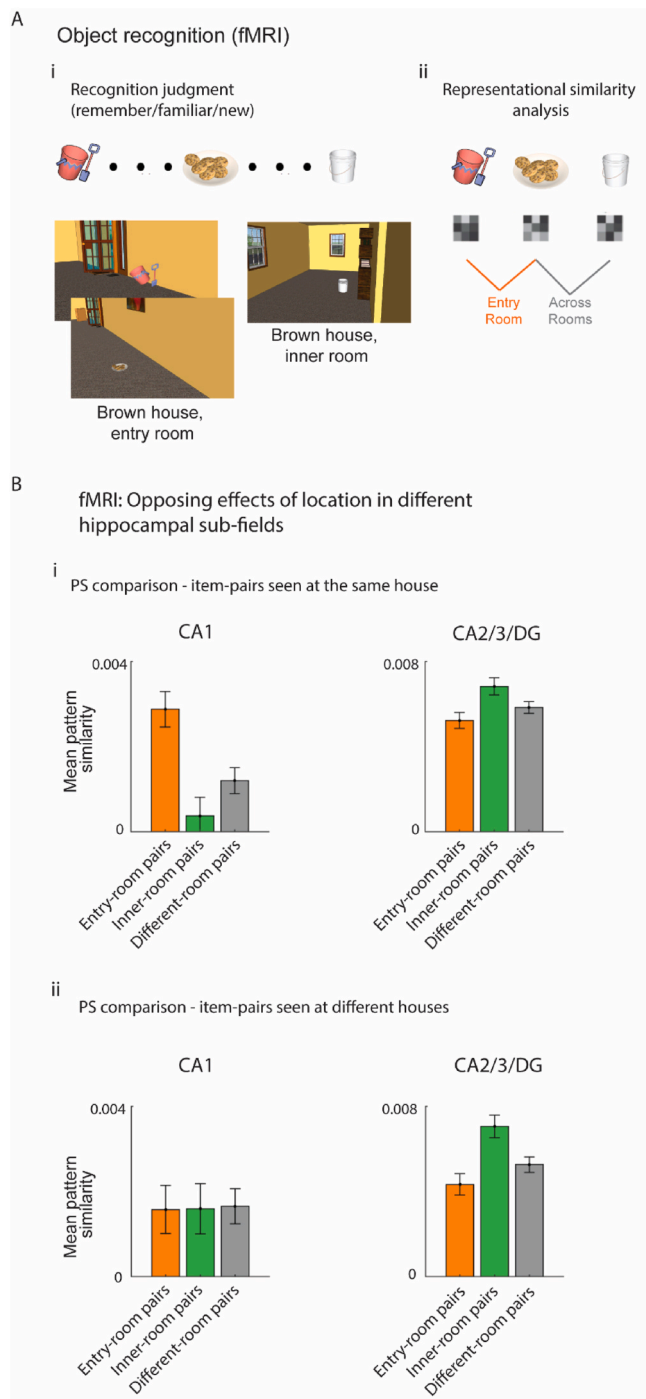
To explore spatial context reinstatement in hippocampal subfields, participants were introduced to a virtual reality environment consisting of two houses, each house containing two rooms (spatial contexts; Fig. 1A–B). After becoming familiarized with the appearance and spatial layouts of each house, which differed in their color and rooms' aspect ratio (but were equal in overall exploration space, Fig. 1B), participants viewed a series of 10 videos presenting first-person navigation through each house, encountering a series of 10 unique objects in each video (Fig. 1A). The virtual tour passively led viewers through the houses, starting with an entry room, continuing to an internal room, and backtracking to exit the house through the entry room.

Subjects' memory performance was evaluated during three phases of the experiment – during encoding, in the fMRI scanner, and during a final post-scan test. During encoding, at the end of each video viewing, participants were asked to judge objects' value and to place the objects

they saw in the video on a bird's eye map of the house (Fig. 1B). Note that each video was viewed once and no feedback was given on the placement test. Following this study phase, participants performed an object recognition test that required them to differentiate between studied and novel objects while undergoing fMRI scanning. Critically, during the scanned object recognition phase, objects were presented in isolation devoid of any explicit contextual information from encoding. Lastly, back in the lab, in a third testing phase which was performed immediately after MRI scanning, subjects were asked to recall where (house and room) every object had been studied.

Behavioral results have been previously reported extensively by Dimsdale-Zucker et al. (2018), so we will only briefly summarize here the key findings relevant to the current re-analysis. First, at the end of each video viewing, during the encoding phase, subjects indicated the correct room for each object with very high probability (correct room placement rate =  $0.96 \pm 0.02$  [mean  $\pm$  std]), 75% of the objects viewed were correctly placed in the correct room by all participants in this immediate test, Sup Fig. 2A). Second, recognition memory performance was measured by evaluating responses to new and old objects during fMRI scanning. Hit-rate was high with some variability between subjects' performance ("remember" hit rate =  $0.66 \pm 0.17$  [mean  $\pm$  std], Sup Fig. 2B (Dimsdale-Zucker et al., 2018)).

Based on previous studies reporting enhanced recognition of objects



(caption on next column)

**Fig. 2. Pattern similarity in CA1 and CA23DG reflects proximity to spatial and temporal boundaries.** (A) (i) **Experimental design:** Subjects were scanned (high-resolution fMRI) while performing an object recognition test. Objects were presented without any contextual information (top). The images below depict the locations the example objects were seen during the encoding session. (ii) Representational similarity analyses (RSA) was used to compare multi-voxel patterns elicited by each recollected object relative to other recollected objects based on their spatial context. (B) **fMRI:** (i) Pattern similarity was calculated for regions of interest corresponding to CA1 and a combined CA2/CA3/dentate gyrus (CA23DG) subregion within the body of hippocampus (Methods). Same house pairs: Pattern similarity was highest in CA1 subfield for object pairs from the same house when located in the entry room relative to inner-room pairs and pairs of objects viewed in different rooms. CA23DG showed a different pattern such that pattern similarity was lower for object pairs seen in the entry room of the same house relative to inner room pairs. (ii) Different house pairs: CA23DG - pattern similarity was lower for object pairs when both were seen in the entry room (close to the event boundary) of different houses relative to inner room objects, while no significant difference was found in CA1. The effect in CA23DG could stem from reduced overlap for entry-room pairs or increased overlap between inner-room pairs which was higher than overlap between different-room pairs.

that were presented around event boundaries (Newtson and Engquist, 1976; Schwan et al., 2000), we compared memory performance for objects presented in the entry room against objects presented in the internal room of the house. Analyses of the behavioral data revealed superior performance for objects residing in the entry room in three separate phases of testing: (i) At the end of each video viewing, during the encoding session, participants placed objects they had seen in the entry room with higher accuracy than objects viewed in the internal room (Fig. 1C, paired Wilcoxon test,  $P < 10^{-4}$ ). (ii) During MRI scanning, when participants were asked to recognize previously learned objects, objects in the entry room had a higher (though non-significant) probability of being recollected relative to objects located in the internal room (paired Wilcoxon test,  $P = 0.06$ ). (iii) In the last testing phase, following the MRI scan, subjects' memory of the house the object was viewed in was significantly higher for entry room objects (Wilcoxon signed-rank test,  $P = 0.0014$ , Fig. 1Cii).

We considered the possibility that recency or primacy effects (Ebbinghaus, 1885) may explain the superior accuracy when recalling the location of objects in the entry room, relative to internal room ones, and whether the superiority was strictly found in the temporal aspect of the memory (order of events), rather than a better spatial source memory. As room identity overlaps with the order of viewing of objects within a video clip (i.e. a subject can infer the room location based on the time an object was seen), these effects could indeed underlie the superior memory of entry room objects in the encoding and MRI test phases. However, the house identity cannot be inferred from the viewing order, so superior memory for entry-room objects' house identity (Fig. 1Cii), suggests a better spatial context memory was acquired for entry-room objects relative to the inner-room ones. Taken together, these behavioral results suggest that subjects acquired a more comprehensive memory of entry-room objects, relative to the inner-room objects, and that the privileged memory status of entry-room objects persisted from the encoding phase to the last phase of testing (a couple of hours later).

## 2.2. Proximity to boundaries shapes neural overlap in hippocampal subfields

We expected recollection-based item recognition to trigger reactivation of information about the context in which that object was encountered (Deuker et al., 2013; DuBrow and Davachi, 2016; Eichenbaum et al., 2007; Miller et al., 2013; Nielson et al., 2015). Accordingly, we tested whether multi-voxel patterns elicited during object recollection, presented without any house/video information, carried information about the associated spatial location for each object. To do this, we

used Representational Similarity Analysis (RSA) (Dymsdale-Zucker and Ranganath, 2018; Kriegeskorte et al., 2008) to measure the similarity of fMRI multi-voxel patterns.

We estimated single-trial multi-voxel patterns within regions of interest corresponding to CA1 and a combined CA2/CA3/dentate gyrus (CA23DG) subregion within the body of hippocampus (Methods). We then computed voxel pattern similarity (PS) between trial pairs for successfully recollected objects. Having discovered that spatial memory accuracy was behaviorally enhanced for entry room objects relative to the internal room ones (Fig. 1C), we tested whether hippocampal activity patterns might disproportionately carry information about the location of objects encountered in the entry room, as compared with objects from the inner room. We restricted the analysis to object recognition trials that were associated with accurate spatial memory (i. e., objects placed in the correct house and room) during the encoding phase (Sup. Fig. 2A). We calculated PS for pairs of objects that were seen in the same house, separately for pairs of objects encountered in the entry room, pairs of objects encountered in the inner room, or pairs that were encountered in different rooms of the same house. To control for the possibility that any observed effects are attributed to temporal context (these effects were previously reported in (Dymsdale-Zucker et al., 2018)), we eliminated trial pairs that had been studied within the same video to ensure that any observed effects could uniquely be attributed to spatial context.

To test whether hippocampal subfields carried information about an object's spatial location, we fitted a linear mixed effect model with a random effect of Subject (Gordon et al., 2014) testing for effects of ROI (CA1 and CA23DG), Spatial location in the house (entry room vs. inner room vs. different room), as well as their interactions on multivoxel PS (Methods). Adding hemisphere as another factor did not reveal a significant interaction so the reported analyses are aggregated across the two hemispheres. We found a highly significant interaction between ROI x Spatial location in the house ( $\chi^2(2) = 25.54, P < 10^{-4}$ ).

To unpack this interaction, we used a mixed effects model to test effects for object-pairs' PS as a function of Spatial Location (same house: entry room vs. inner room vs. different room) separately for each ROI. For both CA1 and CA23DG, there was a significant effect of Spatial location in the house<sup>2</sup> (Fig. 2Bi<sup>3</sup>, Mixed effects model, CA1:  $\chi^2(2) = 14.39, P = 0.0007$ ; CA23DG:  $\chi^2(2) = 7.54, P = 0.02$ ). In CA1, activity patterns were more similar for item pairs seen in the entry room than for objects seen in the inner room ( $\chi^2(1) = 13.70, P = 0.0002$ ) and for objects seen in different rooms ( $\chi^2(1) = 13.70, P = 0.003$ ). These results are consistent with the idea that activity patterns in CA1 carry information about the entry room as a spatial context. In contrast, in CA23DG, pattern similarity was higher for inner room pairs than entry room pairs, ( $\chi^2(1) = 7.27, P = 0.006$ ), but there was no significant difference between inner room pairs and pairs of objects encoded in different rooms ( $\chi^2(1) = 1.4, P = 0.22$ ). Although these results indicate that CA23DG pattern similarity was sensitive to the particular room that an object was encountered in, there was no strong evidence for a spatial context representation per se, because neither entry room nor inner room pairs differed from across-room pairs.

We next compared PS values between pairs of objects encoded in the entry room of the same house and pairs of entry room objects from different houses. This analysis revealed a marginal effect of house identity for item pairs located in the entry room in CA1 ( $\chi^2(1) = 3.44, P = 0.063$ ), with numerically higher pattern similarity for same house entry room item pairs. This effect did not reach significance in CA23DG

<sup>2</sup> We have also conducted statistical analysis using one-way ANOVA which corroborated these results.

<sup>3</sup> For ease of visualization, for pattern similarity comparisons we have chosen to plot means with error bars (standard error of the mean) to illustrate the observed data. This does not exactly recapitulate the way the statistical comparisons were computed since these were performed as mixed effects models.

( $\chi^2(1) = 1.9, P = 0.16$ ).

We next investigated the possibility that subfields might encode a general representation of information encoded close to a boundary. For instance, it is conceivable that the hippocampus could encode objects as having been in an entry room, as opposed to encoding a representation of an object that was encountered in a specific room of a specific house. To test this possibility, we performed the same analyses described above but restricted our analyses to objects encountered in different houses. Interestingly, this analysis revealed a significant effect of Spatial location (different house: entry room vs. inner room vs. different room) in the house for CA23DG ( $\chi^2(2) = 12.67, P = 0.001$ ), but not in CA1 ( $\chi^2(2) = 0.06, P = 0.9$ ; see Fig. 2Bii<sup>2</sup>). Follow-up tests to break down the effect of Spatial Location in CA23DG revealed that pattern similarity was higher for inner room pairs than entry room ( $\chi^2(1) = 12.68, P = 0.0003$ ) or different room ( $\chi^2(1) = 6.96, P = 0.08$ ) pairs.

Our data suggest that CA1 and CA23DG represented different aspects of the room contexts. CA1 activity patterns were consistent with a privileged representation of the entry room within each house. CA23DG activity patterns, in contrast, seemed to reflect information common to any object in an inner room.

### 2.3. Exploratory analysis - neural spatial sensitivity in aPHC and subiculum

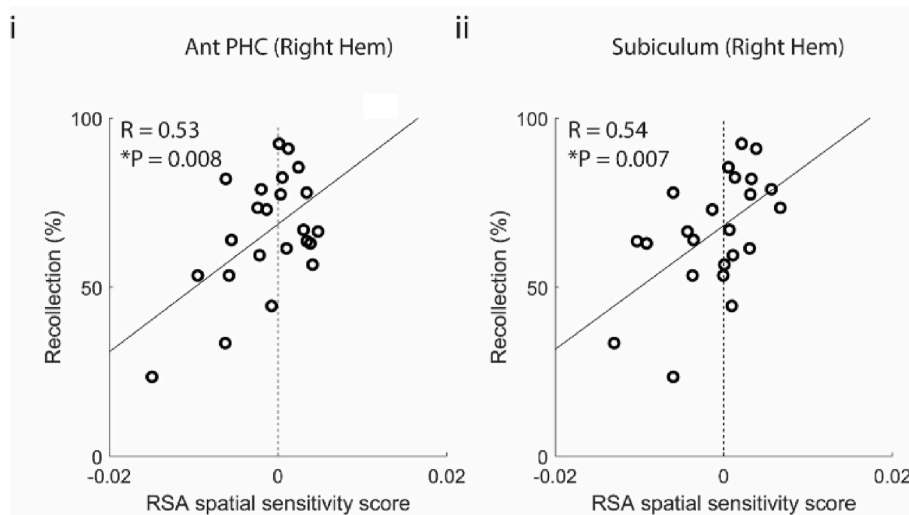
Dymsdale-Zucker et al. (2018) focused on results from CA1 and CA23DG, leaving open the question of whether spatial context information might be incidentally reinstated in other MTL subregions that have been associated with successful recollection. To address this question, we ran a series of exploratory, post-hoc analyses to develop hypotheses that can be tested in future studies. We focused our analysis on two subregions that have been implicated in episodic memory and navigation - the anterior parahippocampal cortex (aPHC) (Aminoff et al., 2013; Baldassano et al., 2016; Bar et al., 2008; Diana et al., 2007; Eichenbaum et al., 2007; Epstein, 2008; Epstein and Baker, 2019; Suzuki and Amaral, 2004) and the subiculum (Amaral and Lavenex, 2007) (see Supplementary Fig. 1 and Methods for segmentation process).

We first examined whether, as in the hippocampus, aPHC and subiculum might carry information about entry- or inner-room objects. A mixed effects model revealed no effects of spatial location, suggesting that there was no significant sensitivity to proximity to spatial or event boundaries as we found in hippocampal subfields. We then examined whether voxel pattern information in these areas might carry spatial information at a more coarse level, reflecting the recollected spatial context (house) associated with each object. To address this question, we computed a 'spatial sensitivity score' by calculating the difference between the median PS values of objects located in the same room of the same house, relative to objects from different rooms in different houses (Fig. 1Cii). However, when aggregating trials from all subjects, we did not find a significant spatial sensitivity score in aPHC nor subiculum.

We next explored the possibility that this null finding was due to interindividual differences in spatial memory accuracy (Supplementary Fig. 2). Consistent with this hypothesis, we found a significant correlation between the 'spatial sensitivity score' and recollection success (hit-rate) per subject in both right hemisphere's aPHC (Pearson correlation:  $R = 0.53, p = 0.008$ , Fig. 3i) and subiculum (Methods, Pearson correlation:  $R = 0.54, p = 0.007$ , Fig. 3ii). We did not observe a significant correlation for responses in the left hemisphere for either region. Overall, results from these exploratory analyses suggest that aPHC and subiculum carry information about recollected spatial contexts at a relatively coarse level and that these representations were tied to higher spatial memory accuracy.

## 3. Discussion

Boundaries are thought to be useful to parse continuous experiences into meaningful chunks in space and time (Kurby and Zacks, 2008; Lu



**Fig. 3. ‘Spatial sensitivity score’ of aPHC and Subiculum is tightly correlated to recollection performance during fMRI scan.** Spatial sensitivity score was defined as the difference between medians of pattern similarity values for objects from the same house and room vs different rooms in different houses (the largest spatial difference obtained in the experienced virtual-reality space). We found a tight correlation between this measure and recollection success (hit-rate) per subject – recollection success was a predictor of spatial sensitivity as reflected by neural pattern similarity in anterior PHC (i) and subiculum (ii) in the right hemisphere. Each circle represents one subject, R and P values for Pearson correlation are calculated over all subjects ( $n = 23$ ).

et al., 2022), and accumulating evidence suggests hippocampal activity is enhanced during the perception of boundaries in naturalistic events (Baldassano et al., 2017; Ben-Yakov and Henson, 2018; Cohn-Sheehy et al., 2021; Reagh et al., 2020; Yoo et al., 2022; Zheng et al., 2022). Spatial boundaries are crucial for navigation and are over-represented by neural activity during active and virtual behavior (Barry et al., 2006; Bird et al., 2010; Doeller et al., 2008; Julian et al., 2018; Julian et al., 2018; Lever et al., 2009; Savelli et al., 2008; Solstad et al., 2008). Here, simulating the exploration of two spaces, combined with object recognition testing in a high-resolution fMRI paradigm, we found that spatial context memory was enhanced for objects in proximity to a boundary and that CA23DG and CA1 showed qualitatively different representations of retrieved spatial context for these objects. Our results suggest that, while in CA1, representations of the spatial context associated with objects are modulated by proximity to boundaries, CA23DG is more informative with respect to event boundaries.

### 3.1. Contextual representations associated with entry room objects in CA1

Dimsdale-Zucker et al. (2018) previously demonstrated that CA1 exhibited increased representational overlap for objects sharing an episodic context (i.e., objects seen in the same video), while CA23DG exhibited greater PS for objects from distinct as compared to shared episodic contexts. However, analyses reported by Dimsdale-Zucker et al. (2018) revealed no evidence of spatial context representation in these subfields. The present analyses were designed to more precisely characterize spatial context representation in the hippocampus in the following way: First, we restricted our analysis to objects for which subjects demonstrated accurate spatial memory. Second, we only calculated PS across pairs of objects seen in different videos to identify spatial context representations in the absence of any shared episodic context. Third, and most importantly, we differentiated between activity elicited by objects that were encountered in the entry room, which was both an environmental boundary and an episodic event boundary in these videos, and the inner room of each house. The latter factor was critical, as we identified a spatial memory advantage for objects encountered in the entry room, as well as the reinstatement of the entry-room context in CA1 during the recollection of studied objects.

It is important to note that our paradigm was not optimized to differentiate between the effects of spatial boundaries and other temporally-based effects. Because entry room objects were encountered at the beginning and end of each movie, proximity to the entry room was confounded with proximity to a temporal/event boundary as well as the spatial boundary for the entry and exit of the house. Previous studies have demonstrated that objects near the start and end of videos (which

can be considered temporal event boundaries) tend to be better remembered (Newton and Engquist, 1976; Schwan et al., 2000), and temporal boundaries can elicit benefits in verbal learning that are comparable to effects of spatial boundaries (Logie and Donaldson, 2021). Another relevant factor is that the entry room was visited both at entry and exit of the house. It is therefore conceivable that the entry room objects were more memorable due to spaced encoding (Antony et al., 2023; Cepeda et al., 2006). While all these factors would enhance the overall memorability for objects in the entry room, for reasons we outline next, a global, nonspecific effect of memorability is insufficient to explain the pattern of results in CA1.

Our results suggest that CA1 activity patterns carried information about spatial context over and above simply being at the beginning or end of a movie. Pattern similarity in CA1 was increased for entry room objects from the same house, but no significant effect was observed when comparing pattern similarity between object pairs from entry rooms and objects originating from different rooms from separate houses. Thus, our results suggest that the CA1 representations of entry room objects had a spatial component. Second, we note that the spatial context reinstatement effect was not globally seen throughout the hippocampus—CA23DG had a qualitatively different pattern of results. Third, we note that Dimsdale-Zucker et al. (2018) found enhanced pattern similarity in CA1 for objects encountered in the same movie, regardless of entry room status. Thus, it is not the case that all contextual representations were modulated by entry room status, even though objects in entry rooms were associated with better overall memory performance. These factors suggest that CA1 carries spatial context information about items that are proximal to boundaries, though we cannot make strong statements about whether such representations are differentially impacted by spatial boundaries and more abstract event boundaries. The present results are broadly consistent with evidence from both animal models and human studies suggesting the importance of environmental boundaries in navigation (Julian et al., 2018) and memory (Anderson and Schooler, 1991; Horner et al., 2016; Radvansky et al., 2011). In rodents, studies have found cells that signal borders in subiculum and medial entorhinal cortex (Hartley et al., 2014; Lever et al., 2009; Solstad et al., 2008). In humans, environmental boundaries serve as a primary cue for reorientation when one loses their bearing (Cheng et al., 2013; Epstein et al., 2017) and boundary-related neural signatures have been observed using fMRI and intracranial electroencephalographic (iEEG) recordings (Bird et al., 2010; Doeller et al., 2008; Julian et al., 2018; Lee et al., 2018; Shine et al., 2019; Stangl et al., 2021). An interaction between spatial boundaries in virtual-reality tasks and long-term memory has been shown before to negatively impact object order retrieval when boundaries break the encoding process

(Horner et al., 2016; Radvansky and Copeland, 2006), suggesting that subspaces in virtual environments are perceived as separate episodic and spatial contexts.

Available evidence also suggests that more abstract event boundaries modulate hippocampal context representations. In films and narratives, changes in a spatial context are reliably associated with subjective event boundaries, but people also identify event boundaries when new characters are introduced, when a temporal shift is implied, or when a goal is attained (Zacks et al., 2009). Notably, several studies have shown that hippocampal activity increases and concomitant with activity pattern shift in high-order areas (including angular gyrus and posterior medial cortex) (Baldassano et al., 2017; Ben-Yakov and Henson, 2018) is thought to reflect changes in online event representation. Moreover, hippocampal activity increases at event boundaries (Cohn-Sheehy et al., 2021; Reagh et al., 2020; J. Zheng et al., 2022) and both activity increases and functional connectivity increases between the Posterior Medial Network and hippocampus at event boundaries are associated with successful event encoding (Barnett et al., 2022; Hahamy et al., 2023). One way to interpret all these findings is that the perception of event boundaries and crossing environmental boundaries are associated with enhanced cortico-hippocampal interactions that support encoding of item-context associations. The latter component is likely to include information about spatial, temporal, and situational contexts.

Several previous studies described above have investigated neural correlates of spatial memory in the hippocampus. The present study differs in two ways from previous work. First, we did not directly assess spatial memory or navigation, but, instead, examined incidental retrieval of spatial context representations during an object-recognition test. Thus, our study was intended to assess how recollection of previously encountered objects leads to recovery of associated contextual information (Diana et al., 2007; Eichenbaum et al., 2007)—i.e., “pattern completion” (Marr, 1971). The second key difference was that each spatial context (i.e., each house) consisted of two rooms, whereas previous studies, to our knowledge, examined activity associated with open environments (Deuker et al., 2016; Kyle et al., 2015; Peer and Epstein, 2021; Steemers et al., 2016; Stokes et al., 2015; L. Zheng et al., 2021), single rooms (Guo et al., 2021), or adjoining rooms within a single context (Hassabis et al., 2009; Kim and Maguire, 2018). This distinction turned out to be important because PS values in CA1 were greater for pairs of objects that were located in the entry room of the same house than for pairs of objects in the inner room or objects encountered in different rooms. This finding only applied to objects that were in the same house—objects that were in the entry rooms of different houses did not show pattern similarity increases. Accordingly, these results suggest that, during recollection, CA1 patterns carried information about the specific spatial context in which entry room objects were encountered.

### 3.2. Contextual representations in CA23DG, subiculum, and aPHC

Results in CA23DG were qualitatively different from those in CA1. Unlike CA1, we did not see any evidence for a significant spatial context representation of the entry room, and PS for entry room objects was lower than for inner room objects (Fig. 2B, right panels). The reduction in pattern similarity between entry-room objects relative to inner-room pairs was evident regardless of whether the objects were in the same or different houses. There are at least two ways to explain this pattern of results. One option would be that CA23DG representations of objects that appeared in an entry room (of any house) were pulled apart from one another over the course of learning. This would be consistent with prior reports of hippocampal “repulsion” (Chanales et al., 2017; Ritvo et al., 2019) in which neural representations of overlapping memories are hyper-differentiated from one another. Alternatively, it is possible that CA23DG preferentially encoded a common contextual representation for any object that was encountered in an inner room (i.e., far from an event boundary). The present results do not allow us to make strong

interpretations in favor of either account. That said, the different patterns of results in CA1, as compared with CA23DG, suggest the need for future research investigating the extent to which spatial representations may be shared, hyper-differentiated, or abstracted.

In addition to investigating activity in CA1 and CA23DG, we also conducted exploratory analyses of spatial representations in aPHC and subiculum. These areas are major input and output hubs of the hippocampus (Aggleton et al., 2010; Amaral and Lavenex, 2007; Burwell, 2000; Epstein, 2008; Kravitz et al., 2011; Ranganath and Ritchey, 2012; van Strien et al., 2009), and known to play an important role in spatial and episodic memory (Eichenbaum et al., 2007; Ekstrom and Ranganath, 2018; O'Mara et al., 2009). For example, Hassabis et al. (2009) examined activation while participants navigated a virtual environment consisting of two connected square rooms and found that activation patterns in parahippocampal cortex distinguished between the rooms. To identify whether fMRI responses in our study reflect the similarity of locations in the virtual space (defined by the house and room identity), we compared PS overlap for item pairs from the same house/room vs item pairs from different houses/rooms. Interestingly, we observed a robust correlation in these areas between individual hit-rate in the recognition task and a difference in PS values for item pairs from same/different spatial contexts. It is important to reiterate that these analyses in subiculum and aPHC were post-hoc and exploratory, but the results are sufficient to motivate future work to characterize spatial and episodic memory representations in the broader parahippocampal region (Witter et al., 1989). We note that similar results were found in the posterior medial entorhinal cortex, although data from this area was not reported because it did not meet our data quality thresholds (Methods).

### 3.3. Future directions

The present results suggest several fruitful directions for future research. One key question concerns the representations that support memory for item-context associations and those that are used to make temporal order judgments. Some studies have reported complex effects of abstract event boundaries (DuBrow and Davachi, 2016; Pu et al., 2022) and environmental boundaries (Horner et al., 2016; Radvansky and Copeland, 2006) on memory for temporal order information. For instance, Horner et al. (2016) reported that the relative order of two objects encountered in the same room in a virtual reality environment is more accurately remembered than a sequence of two objects presented in adjoining rooms, suggesting that the presence of a spatial boundary at encoding (a doorway between two rooms) impairs subsequent recollection of the temporal order that objects were presented in. Thus, proximity to boundaries seems to facilitate memory for certain kinds of item-context associations while disrupting the ability to make accurate attributions about the temporal contexts associated with different items (DuBrow and Davachi, 2016; Pu et al., 2022). This finding may be consistent with computational models suggesting that temporal context representations can be disrupted by changes in task or environmental context (Antony et al., 2023; Polyn et al., 2009).

A second key question concerns potential differences between hippocampal subfields and the extended cortico-hippocampal network that includes the subiculum, retrosplenial, medial prefrontal, and medial temporal cortex (Aggleton et al., 2010; Ranganath and Ritchey, 2012). Do different boundary-related signals in these brain areas reflect a hierarchy in event segmentation computations, such that fine-to-coarse segmentation is associated with different components of this brain network? A recent study provides some evidence for this theoretical framework: by performing iEEG recordings in humans viewing a series of short video clips researchers revealed different types of cells, sensitive to transitions in the movies, classified as two types of event boundaries (Zheng et al., 2022). Cells that responded to a start or end of a video clip (coined as ‘sharp’ event transitions), were more common in the hippocampus, and cells that also respond to softer, conceptual transitions within a video (which can be seen as equivalent to movement between



rooms in our passive exploration task) were more common in extrahippocampal areas (Zheng et al., 2022). In our dataset, multi-voxel activation in CA1/CA23DG was sensitive to the hard spatial/temporal boundary, and extrahippocampal activity was more informative of general spatial location in virtual space. Taken together with the electrophysiological correlates described, our data is in line with a hierarchical model for event segmentation, in which the extrahippocampal information reflects contextual changes detected in high-level visual areas (Aminoff et al., 2013; Isik et al., 2018), while the hippocampal cells provide a coarse segmentation, that may reflect a comparator operation between predicted and received signals (Lisman and Grace, 2005; Vinogradova, 2001; Y. Zheng et al., 2021). This model would predict differences in parsing continuous experiences between patients suffering from hippocampal atrophy and patients with parahippocampal atrophy.

Recent research proposes spatial schemas (Farzanfar et al., 2023) as a powerful perspective to capture prior knowledge of common patterns across related spatial experiences. For example, a schema would capture the viewers' expectations from a typical two-room suburb house that was used in our virtual paradigm. While spatial-schemas were suggested to be supported by neocortical areas (Peer and Epstein, 2021; L. Zheng et al., 2021), gist-like representations are expected to be found in hippocampal areas (Tse et al., 2007). Previous studies using fMRI in humans navigating comparable environments have assessed whether spatial-schemas would describe effects in hippocampal and neocortical areas (He et al., 2021; Peer and Epstein, 2021; L. Zheng et al., 2021). In most studies, the assessment is done during a spatial-judgment task (for example planning a path or determining a direction to a tested location). However, a recent study (Peer and Epstein, 2021) has also looked assessed multi-voxel overlap between hippocampal responses during object viewing. Peer et al. found that neural activity in the left anterior hippocampus during an object viewing task fit a schematization model of two symmetric environments separated by a natural boundary. How do our results fit this line of work? In our case, the two environments (houses) used in the study were different in terms of the aspect ratio (Fig. 1B). The rooms were equal in size in every house but different between houses. A schematization model may predict a similar relative organization of the two houses but the visual differences are a caveat that limits this analysis in our case. An additional limitation is that our subspaces are not large enough to allow a robust comparison of encoding patterns in different parts of each subspace. Follow-up studies that use larger rooms, dense resolution of object placement, and different access points to the house, would be required to tease these effects apart. Furthermore, the high-resolution scan we used did not include prefrontal cortex areas that would be a natural target for exploring spatial-schema development for the environments used, and thus limit our ability to assess whether spatial codes can be revealed in prefrontal areas during recollection.

The development of high-resolution fMRI, as an approach to studying human MTL functions (Bakker et al., 2008; Carr et al., 2010; Zeineh et al., 2003), enabled dissociation of differential roles of hippocampal subfields in memory encoding and retrieval processes in humans. Our results are consistent with previous studies demonstrating a dissociation between CA1 and CA23DG during recollection of contextual information (Dimsdale-Zucker et al., 2018). Our results are largely in line with a model suggesting that CA1 activity reflects a reconstruction of stored patterns in response to an incomplete cue ("pattern completion"). In our study, this reconstruction was revealed during recollection for highly memorable items while not revealed in our study for the less memorable, inner-room items. For these memorable item pairs, we found that CA23DG exaggerates differences between items within the same context ("pattern separation"). This suggests hippocampal subfields may play complementary roles when encoding the context items shared.

#### 4. Conclusions

One of the hallmarks of episodic memory is the ability to bring to mind a coherent representation of the elements of an event, even when these elements are incidental to the retrieval condition (Tulving et al., 1983). Our findings complement previous studies that revealed hippocampal reinstatement of neural activity during a recognition task in intracranial patients (Miller et al., 2013) and in fMRI studies (Chadwick et al., 2011; Kyle et al., 2015; Zeidman and Maguire, 2016; L. Zheng et al., 2021) during tasks that involve intentional recollection of the spatial locations in which objects were studied. Our results indicate that, during recollection, just as Tulving posited, spatial information is retrieved and reflected both in MTL subregions (aPHC and subiculum) and hippocampal subfields (CA1 and CA23DG), even when incidental to the recognition task.

#### 5. Methods

**Participants.** Analyses presented are from 23 participants ( $N_{\text{female}} = 11$ ,  $N_{\text{male}} = 12$  based on self-reporting, mean age = 19.5 years), the same cohort described in Dimsdale-Zucker et al. (2018).

**Stimuli and materials.** Study materials included two virtual houses, each divided into two rooms, which were created in Google SketchUp (<https://www.sketchup.com/>, version 15.3.329, all stimuli are freely available – OSF | [abcdcon\\_pub](https://osf.io/5th8r/), <https://osf.io/5th8r/>). The two houses differed in their exterior color, wall color, room orientation, and decoration style (Fig. 1B). Though they differed in their aspect-ratio houses were matched in their total virtual square area. Each house contained ten pieces of landmark furniture that shared semantic labels (e.g., "couch") but differed in appearance (e.g., angular gray couch vs. plush green couch). Three hundred neutral objects (e.g., football helmet, suitcase, teddy bear) were selected from the Google SketchUp image library. Two-hundred and forty of these objects were randomly selected and the rest were used as lure objects (see below). Object assignment was random and was house- and video-unique so that 12 lists, each consisting of 10 objects, were assigned to each house. To determine object placement, rooms were divided into eighths, all possible combinations of five positions were generated, and objects were randomly assigned to one of these combinations. Thus, object configurations within each room (and thus within each house) were video-unique. Videos depicting trajectories through the houses were generated using Google SketchUp's animation feature. Videos were exported for each house both with landmark furniture only and for each of the 12 videos with objects within each home. Trajectories did not change between videos within a home and followed a path that started at the main door circling the entry room, then crossing another door to the internal room, and backtracking to exit via the main door. Each video was approximately 1 min 40 s in duration.

**Experimental procedure:** After providing informed consent, participants completed four experimental phases which were reported previously (Dimsdale-Zucker et al., 2018) and summarized here:

- (i) Spatial context familiarization: Participants were acquainted with two different houses and were then given up to 10 min to draw a map of each house to ensure thorough knowledge of spatial layouts (including the location of doors, walls, and furniture). Their drawings were reviewed by the experimenter to ensure any mistakes (although rare) were corrected.
- (ii) Object encoding: During this phase, participants viewed a series of 20 videos, each depicting passive navigation through one of the two spatial contexts (brown or gray house, Fig. 1B), with ten different objects placed along the pre-defined trajectory. At the end of each video, a still frame of each of the ten objects viewed in the house appeared one at a time in random order for 4 s while the participant judged whether the object was worth more than \$50 (yes/no). After making this value judgment, the still frame of

the object was replaced by a birds-eye-view perspective map of the house where each room was divided into quadrants with numeric labels. Participants indicated the quadrant number where the object had been located during the video via keypress (1–8). In total, participants saw ten videos in each house presented such that the order of the houses alternated (e.g., house1/video1, house2/video2, house1/video3, house2/video4, etc.). The ten videos were randomly selected from the pool of 12 videos in each house and the order of video presentation was uniquely randomized for each participant. The encoding phase took roughly 1 h to complete.

- (iii) Object recognition test (fMRI): this phase took place across four runs in the MRI scanner following the acquisition of structural scans. Sixty-three still images were presented in each run for 3 s with a jittered inter-trial interval ranging from 2 to 8 s. All 200 studied objects were presented with an additional 52 new, unstudied objects. New objects were randomly selected from a pool of objects that were not presented in either house. While the image was on the screen, participants made recognition judgments (“remember”, “feels familiar”, “new”) via an MRI-compatible button box. Participants were instructed to make a “remember” response when they could recall a specific detail from when they had studied the object (Yonelinas, 2002), “feels familiar” if they thought they had studied the object but were unable to retrieve a specific detail and “new” for objects that they did not think they had studied during object encoding. Critically, no house or video information was re-presented to participants in these object images.
- (iv) Spatial context memory test: Participants were brought back to the lab to complete testing. In this phase, participants were re-presented with the 200 studied objects, and they were asked to recall where (house and room) each object had been studied. Images remained on the screen for 3 s while participants made their responses. There was no opportunity to skip a spatial judgment.

**fMRI acquisition and preprocessing.** Scan properties, preprocessing pipeline, and quality assurance process were extensively described in Dimsdale-Zucker et al. (2018). Quality assurance (QA) included evaluating signal-to-noise ratio (SNR) for included ROIs via custom code (<https://github.com/memobc/memolab-fmriqa>) (Kaufman et al., 1989).

**ROI segmentation.** Hippocampal subfield ROIs segmentation was described in (Dimsdale-Zucker et al., 2018) and summarized here. The ASHS toolbox (Yushkevich et al., 2010) with the UPenn atlas was used to create segmented ROIs, which were co-registered to the mean functional image and split into masks for each ROI of interest. We took a conservative segmentation approach in which we combined subfields DG, CA3, and CA2 into a combined region based on prior high-resolution fMRI work (Dimsdale-Zucker et al., 2018; Ekstrom et al., 2009; Stokes et al., 2015; Yushkevich et al., 2010). Head, body, and tail were manually defined but subfield comparisons were limited to the body where boundaries between CA1 and CA2/3DG can be most clearly and reliably delineated (Dimsdale-Zucker et al., 2018; Yushkevich et al., 2015a, 2015b). The disappearance of the gyrus intralimbicus was used as the head/body boundary (Frankó et al., 2014) and the presence of the wing of the ambient cistern demarcated body/tail (Yushkevich et al., 2015a, 2015b).

Boundaries between PRC, ERC, PHC, and subiculum regions were defined manually on individual participant high-resolution structural images in FSLView according to (Duvernoy, 1998; Insausti et al., 1998; Zeineh et al., 2001) (Supplementary Fig. 1). The PHG mask contained gray matter voxels along the banks of the collateral sulcus. Anterior PHC regions of interest (ROI) extended from the first slice immediately following the PRC, 4 mm following the HC head slice to the slice where colliculi are seen (approximately 5 mm to the end of the HC (Frankó

et al., 2014),) in the anterior-posterior direction, and from the collateral sulcal fundus to the most medial vertex of the parahippocampal gyrus in the lateral–medial direction. PHC ROIs for the right and left hemispheres were created separately by manual tracing of gray matter within these demarcations.

**Data analysis.** ROI summary statistics, including pattern similarity analyses, were computed using custom code implemented in MATLAB r2018a ([www.mathworks.com](http://www.mathworks.com)) and R version 3.3.2 (<http://www.R-project.org>). Statistical comparisons were conducted in Matlab including linear mixed models (LinearMixedModel class, *fitlme()*). Our mixed models included fixed effects of the condition, ROI, and hemisphere as well as a random subject intercept. P-values were obtained by a likelihood ratio test that compares a full model with the effect of interest against a reduced model without this effect (LinearMixedModel class, *compare()*).

**PS analyses.** Pattern similarity (PS) analyses (Kriegeskorte et al., 2008) were conducted on beta maps generated from unsmoothed data in native subject space as described in (Dimsdale-Zucker et al., 2018) and summarized here. Following the procedure described by Mumford et al. (Mumford et al., 2012; Ritchey et al., 2015), single trial models were generated to estimate a unique beta map for every trial in a run (N = 63). Within each single trial model, the first regressor modeled the trial of interest with a stick function, the second regressor modeled all other trials in that run, six regressors were used to capture motion, and any additional spike regressors as identified by our QA scripts were used to capture additional residual variance. Following beta estimation, outlier values were identified by setting a z-scored beta threshold of 0.7–0.85 based on visual inspection of the distribution of z-scored beta values for all subjects. This resulted in an average of 9.87% (mean = 6.22 trials, SD = 7.10 trials) excluded beta values per run for each participant.

Voxel-wise patterns of hemodynamic activity were separately extracted for each ROI from the single trial beta images. Within each ROI, correlations (Pearson’s R) were computed between these trial-wise betas to yield a trial-by-trial correlation matrix that related each voxel’s signal on a trial to all other trials across all runs. Statistical analyses tested for differences in correlations between trial pairs based on encoding location (room and house). Only between-run correlations were used to maximize the number of possible trial pairs without mixing within- and between-run correlations. Trial pairs of interest were extracted from these trial-by-trial correlation matrices. For all conditions, we restricted comparisons to trials in which participants made a correct “remember” response (during MRI scanning), correctly placed the object in the room it was seen in the immediate post-encoding test, and also correctly identified the object’s spatial (house) context (post-MRI spatial source task). To control for the possibility that any observed effects are attributed to temporal context (these effects were previously reported in (Dimsdale-Zucker et al., 2018), we eliminated trial pairs that had been studied within the same video to ensure that any observed effects could uniquely be attributed to spatial context.

Additionally, we used bootstrapping (Westfall and Young, 1993) to validate that the different sizes of groups represented in each bar are not biasing the results. We resampled the larger group  $10^3$  times and compared the medians of the two groups. We verified the sign of the difference between medians matches our reported results in more than 99.95% of the bootstrapped groups.

#### Credit author statement

Maya Geva-Sagiv: Conceptualization, Methodology, Formal analysis, Writing. Halle R. Dimsdale-Zucker: Resources, Software, Supervision, Writing - Review & Editing. Ashley B. Williams: Resources, Writing - Review. Charan Ranganath: Conceptualization, Supervision, Writing - Review & Editing.

## Declaration of competing interest

We have no conflict of interest to disclose.

## Data availability

Data has been shared in public repository and link is included in the manuscript. Custom code is publicly available in a GitHub Repository which is reported in the manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2023.108656>.

## References

- Aggleton, J.P., O'Mara, S.M., Vann, S.D., Wright, N.F., Tsanov, M., Erichsen, J.T., 2010. Hippocampal-anterior thalamic pathways for memory: uncovering a network of direct and indirect actions. *Eur. J. Neurosci.* 31 (12), 2292–2307. <https://doi.org/10.1111/j.1460-9568.2010.07251.x>.
- Amaral, D., Lavenex, P., 2007. Hippocampal neuroanatomy. In: Andersen, P., Morris, R. G., Amaral, D.G., V Bliss, T., O'Keefe, J. (Eds.), *The hippocampus book*. Oxford University Press, pp. 37–115.
- Aminoff, E.M., Kveraga, K., Bar, M., 2013. The role of the parahippocampal cortex in cognition. *Trends Cognit. Sci.* 17 (8), 379–390. <https://doi.org/10.1016/j.tics.2013.06.009>.
- Anderson, J.R., Schooler, L.J., 1991. Reflections of the environment in memory. *Psychol. Sci.* 2 (6), 396–408. <https://doi.org/10.1111/j.1467-9280.1991.tb00174.x>.
- Antony, J., Liu, X.L., Zheng, Y., Ranganath, C., O'Reilly, R.C., 2023. Memory out of context: spacing effects and decontextualization in a computational model of the medial temporal lobe. *bioRxiv*. <https://doi.org/10.1101/2022.12.01.518703>, 2022.12.01.518703.
- Bakker, A., Kirwan, C.B., Miller, M., Stark, C.E.L., 2008. Pattern separation in the human hippocampal CA3 and dentate gyrus. *Science (New York, N.Y.)* 319 (5870), 1640–1642. <https://doi.org/10.1126/science.1152882>.
- Baldassano, C., Esteva, A., Fei-Fei, L., Beck, D.M., 2016. Two distinct scene-processing networks connecting vision and memory. *ENeuro* 3 (5). <https://doi.org/10.1523/ENEURO.0178-16.2016>.
- Baldassano, C., Chen, J., Zadbood, A., Pillow, J.W., Hasson, U., Norman, K.A., 2017. Discovering event structure in continuous narrative perception and memory. *Neuron* 95 (3), 709–721.e5. <https://doi.org/10.1016/j.neuron.2017.06.041>.
- Bar, M., Aminoff, E., Schacter, D.L., 2008. Scenes unseen: the parahippocampal cortex intrinsically subserves contextual associations, not scenes or places per se. *J. Neurosci. : Off. J. Soc. Neurosci.* 28 (34), 8539–8544. <https://doi.org/10.1523/JNEUROSCI.0987-08.2008>.
- Barnett, A.J., Nguyen, M., Spargo, J., Yadav, R., Cohn-Sheehy, B.I., Ranganath, C., 2022. Dynamic hippocampal-cortical interactions during event boundaries support retention of complex narrative events. *bioRxiv*. <https://doi.org/10.1101/2022.10.23.513391>, 2022.10.23.513391.
- Barry, C., Lever, C., Hayman, R., Hartley, T., Burton, S., O'Keefe, J., Jeffery, K., Burgess, N., 2006. The boundary vector cell model of place cell firing and spatial memory. *Rev. Neurosci.* 17 (1–2), 71–97. <https://doi.org/10.1515/revneuro.2006.17.1-2.71>.
- Bastin, J., Vidal, J.R., Bouvier, S., Perrone-Bertolotti, M., Bénis, D., Kahane, P., David, O., Lachaux, J.-P., Epstein, R.A., 2013. Temporal components in the parahippocampal place area revealed by human intracerebral recordings. *J. Neurosci. : Off. J. Soc. Neurosci.* 33 (24), 10123–10131. <https://doi.org/10.1523/JNEUROSCI.4646-12.2013>.
- Ben-Yakov, A., Henson, R.N., 2018. The hippocampal film editor: sensitivity and specificity to event boundaries in continuous experience. *J. Neurosci. : Off. J. Soc. Neurosci.* 38 (47), 10057–10068. <https://doi.org/10.1523/JNEUROSCI.0524-18.2018>.
- Berron, D., Schütze, H., Maass, A., Cardenas-Blanco, A., Kuijff, H.J., Kumaran, D., Düzel, E., 2016. Strong evidence for pattern separation in human dentate gyrus. *J. Neurosci. : Off. J. Soc. Neurosci.* 36 (29), 7569–7579. <https://doi.org/10.1523/JNEUROSCI.0518-16.2016>.
- Bird, C.M., Capponi, C., King, J.A., Doeller, C.F., Burgess, N., 2010. Establishing the boundaries: the hippocampal contribution to imagining scenes. *J. Neurosci.* 30 (35), 11688. <https://doi.org/10.1523/JNEUROSCI.0723-10.2010>. LP – 11695.
- Brown, T.I., Ross, R.S., Keller, J.B., Hasselmo, M.E., Stern, C.E., 2010. Which way was I going? Contextual retrieval supports the disambiguation of well learned overlapping navigational routes. *J. Neurosci. : Off. J. Soc. Neurosci.* 30 (21), 7414–7422. <https://doi.org/10.1523/JNEUROSCI.6021-09.2010>.
- Burwell, R.D., 2000. The parahippocampal region: corticocortical connectivity. *Ann. N. Y. Acad. Sci.* 911, 25–42. <https://doi.org/10.1111/j.1749-6632.2000.tb06717.x>.
- Carr, V.A., Rissman, J., Wagner, A.D., 2010. Imaging the human medial temporal lobe with high-resolution fMRI. *Neuron* 65 (3), 298–308. <https://doi.org/10.1016/j.neuron.2009.12.022>.
- Cepeda, N.J., Pashler, H., Vul, E., Wixted, J.T., Rohrer, D., 2006. Distributed practice in verbal recall tasks: a review and quantitative synthesis. *Psychol. Bull.* 132 (3), 354–380. <https://doi.org/10.1037/0033-2909.132.3.354>.
- Chadwick, M.J., Hassabis, D., Maguire, E.A., 2011. Decoding overlapping memories in the medial temporal lobes using high-resolution fMRI. *Learn. Mem.* 18 (12), 742–746. <https://doi.org/10.1101/lm.023671.111>.
- Chanales, A.J.H., Oza, A., Favila, S.E., Kuhl, B.A., 2017. Overlap among spatial memories triggers repulsion of hippocampal representations. *Curr. Biol. : CB* 27 (15), 2307–2317.e5. <https://doi.org/10.1016/j.cub.2017.06.057>.
- Cheng, K., Huttenlocher, J., Newcombe, N.S., 2013. 25 years of research on the use of geometry in spatial reorientation: a current theoretical perspective. *Psychon. Bull. Rev.* 20 (6), 1033–1054. <https://doi.org/10.3758/s13423-013-0416-1>.
- Cohn-Sheehy, B.I., Delarazan, A.I., Reagh, Z.M., Crivelli-Decker, J.E., Kim, K., Barnett, A. J., Zacks, J.M., Ranganath, C., 2021. The hippocampus constructs narrative memories across distant events. *Curr. Biol. : CB* 31 (22), 4935–4945.e7. <https://doi.org/10.1016/j.cub.2021.09.013>.
- Deuker, L., Olligs, J., Fell, J., Kranz, T.A., Mormann, F., Montag, C., Reuter, M., Elger, C. E., Axmacher, N., 2013. Memory consolidation by replay of stimulus-specific neural activity. *J. Neurosci.* 33 (49), 19373–19383. <https://doi.org/10.1523/JNEUROSCI.0414-13.2013>.
- Deuker, L., Bellmund, J.L.S., Navarro Schröder, T., Doeller, C.F., 2016. An event map of memory space in the hippocampus. *Elife* 5, e16534. <https://doi.org/10.7554/eLife.16534>.
- Diana, R.A., Yonelinas, A.P., Ranganath, C., 2007. Imaging recollection and familiarity in the medial temporal lobe: a three-component model. *Trends Cognit. Sci.* 11 (9), 379–386. <https://doi.org/10.1016/j.tics.2007.08.001>.
- Diana, R.A., Yonelinas, A.P., Ranganath, C., 2013. Parahippocampal cortex activation during context reinstatement predicts item recollection. *J. Exp. Psychol. Gen.* 142 (4), 1287–1297. <https://doi.org/10.1037/a0034029>.
- Dimisdale-Zucker, H.R., Ranganath, C., 2018. Chapter 27 - representational similarity analyses: a practical guide for functional MRI applications. In: T-H, D.B., Manahan-Vaughan, of B.N. (Eds.), *Handbook of Neural Plasticity Techniques*, vol. 28. Elsevier, pp. 509–525. <https://doi.org/10.1016/B978-0-12-812028-6.00027-6>.
- Dimisdale-Zucker, H.R., Ritchey, M., Ekstrom, A.D., Yonelinas, A.P., Ranganath, C., 2018. CA1 and CA3 differentially support spontaneous retrieval of episodic contexts within human hippocampal subfields. *Nat. Commun.* 9 (1) <https://doi.org/10.1038/s41467-017-02752-1>.
- Ding, S.-L., 2013. Comparative anatomy of the prosubiculum, subiculum, presubiculum, postsubiculum, and parasubiculum in human, monkey, and rodent. *J. Comp. Neurol.* 521 (18), 4145–4162. <https://doi.org/10.1002/cne.23416>.
- Doeller, C.F., King, J.A., Burgess, N., 2008. Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proc. Natl. Acad. Sci. U.S.A.* 105 (15), 5915–5920. <https://doi.org/10.1073/pnas.0801489105>.
- DuBrow, S., Davachi, L., 2016. Temporal binding within and across events. *Neurobiol. Learn. Mem.* 134 (Pt A), 107–114. <https://doi.org/10.1016/j.nlm.2016.07.011>.
- Duvernoy, H.M., 1998. *The Human Hippocampus: Functional Anatomy, Vascularization and Serial Sections with MRI*, second ed. Springer Science & Business Media.
- Düzel, E., Habib, R., Rotte, M., Guderian, S., Tulving, E., Heinze, H.-J., 2003. Human hippocampal and parahippocampal activity during visual associative recognition memory for spatial and nonspatial stimulus configurations. *J. Neurosci. : Off. J. Soc. Neurosci.* 23 (28), 9439–9444. <https://doi.org/10.1523/JNEUROSCI.23-28-09439.2003>.
- Ebbinghaus, Hermann, 1885. *Über das Gedächtnis: Untersuchungen zur experimentellen Psychologie*. Verlag von Duncker & Humblot.
- Eichenbaum, H., 2017. On the integration of space, time, and memory. *Neuron* 95 (5), 1007–1018. <https://doi.org/10.1016/j.neuron.2017.06.036>.
- Eichenbaum, H., Yonelinas, A.P., Ranganath, C., 2007. The medial temporal lobe and recognition memory. *Annu. Rev. Neurosci.* 30, 123–152. <https://doi.org/10.1146/annurev.neuro.30.051606.094328>.
- Ekstrom, A.D., Ranganath, C., 2018. Space, time, and episodic memory: the hippocampus is all over the cognitive map. In: *Hippocampus*. <https://doi.org/10.1002/hipo.22750>.
- Ekstrom, A.D., Bazih, A.J., Suthana, N.A., Al-Hakim, R., Ogura, K., Zeineh, M., Burggren, A.C., Bookheimer, S.Y., 2009. Advances in high-resolution imaging and computational unfolding of the human hippocampus. *Neuroimage* 47 (1), 42–49. <https://doi.org/10.1016/j.neuroimage.2009.03.017>.
- Epstein, R.A., 2008. Parahippocampal and retrosplenial contributions to human spatial navigation. *Trends Cognit. Sci.* 12 (10), 388–396. <https://doi.org/10.1016/j.tics.2008.07.004>.
- Epstein, R.A., Baker, C.I., 2019. Scene perception in the human brain. *Annual Review of Vision Science* 5, 373–397. <https://doi.org/10.1146/annurev-vision-091718-014809>.
- Epstein, R.A., Patai, E.Z., Julian, J.B., Spiers, H.J., 2017. The cognitive map in humans: spatial navigation and beyond. *Nat. Neurosci.* 20 (11), 1504–1513. <https://doi.org/10.1038/nn.4656>.
- Essoe, J.K.-Y., Reggente, N., Ohno, A.A., Baek, Y.H., Dell'Italia, J., Rissman, J., 2022. Enhancing learning and retention with distinctive virtual reality environments and mental context reinstatement. *Npj Science of Learning* 7 (1), 31. <https://doi.org/10.1038/s41539-022-00147-6>.
- Farzafar, D., Spiers, H.J., Moscovitch, M., Rosenbaum, R.S., 2023. From cognitive maps to spatial schemas. *Nat. Rev. Neurosci.* 24 (2), 63–79. <https://doi.org/10.1038/s41583-022-00655-9>.
- Frankó, E., Insausti, A.M., Artacho-Pérola, E., Insausti, R., Chavoix, C., 2014. Identification of the human medial temporal lobe regions on magnetic resonance images. *Hum. Brain Mapp.* 35 (1), 248–256. <https://doi.org/10.1002/hbm.22170>.

- Gordon, A.M., Rissman, J., Kiani, R., Wagner, A.D., 2014. Cortical reinstatement mediates the relationship between content-specific encoding activity and subsequent recollection decisions. *Cerebral Cortex* (New York, N.Y. 1991 24 (12), 3350–3364. <https://doi.org/10.1093/cercor/bht194>.
- Guo, J., Zhang, K., Zhang, J., Zhao, R., Liang, Y., Lin, Y., Yu, S., Qin, W., Yang, X., 2021. Decoding spatial memory retrieval in cubical space using fMRI signals. *Front. Neural Circ.* 15, 624352 <https://doi.org/10.3389/fnirc.2021.624352>.
- Guzowski, J.F., Knierim, J.J., Moser, E.I., 2004. Ensemble dynamics of hippocampal regions CA3 and CA1. *Neuron* 44 (4), 581–584. <https://doi.org/10.1016/j.neuron.2004.11.003>.
- Hahamy, A., Dubossarsky, H., Behrens, T.E.J., 2023. The human brain reactivates context-specific past information at event boundaries of naturalistic experiences. *Nat. Neurosci.* <https://doi.org/10.1038/s41593-023-01331-6>.
- Hartley, T., Lever, C., Burgess, N., O'Keefe, J., 2014. Space in the brain: how the hippocampal formation supports spatial cognition. *Phil. Trans. Biol. Sci.* 369 (1635), 20120510 <https://doi.org/10.1098/rstb.2012.0510>.
- Hassabis, D., Chu, C., Rees, G., Weiskopf, N., Molyneux, P.D., Maguire, E.A., 2009. Decoding neuronal ensembles in the human hippocampus. *Curr. Biol.* 19 (7), 546–554. <https://doi.org/10.1016/j.cub.2009.02.033>.
- He, Q., Beveridge, E.H., Starnes, J., Goodroe, S.C., Brown, T.I., 2021. Environmental overlap and individual encoding strategy modulate memory interference in spatial navigation. *Cognition* 207, 104508. <https://doi.org/10.1016/j.cognition.2020.104508>.
- Horner, A.J., Bisby, J.A., Wang, A., Bogus, K., Burgess, N., 2016. The role of spatial boundaries in shaping long-term event representations. *Cognition* 154, 151–164. <https://doi.org/10.1016/j.cognition.2016.05.013>.
- Insausti, R., Juottonen, K., Soininen, H., Insausti, A.M., Partanen, K., Vainio, P., Laakso, M.P., Pitkänen, A., 1998. MR volumetric analysis of the human entorhinal, perirhinal, and temporopolar cortices. *AJNR. American Journal of Neuroradiology* 19 (4), 659–671.
- Isik, L., Singer, J., Madsen, J.R., Kanwisher, N., Kreiman, G., 2018. What is changing when: decoding visual information in movies from human intracranial recordings. *Neuroimage* 180 (Pt A), 147–159. <https://doi.org/10.1016/j.neuroimage.2017.08.027>.
- Julian, J.B., Keinath, A.T., Frazzetta, G., Epstein, R.A., 2018a. Human entorhinal cortex represents visual space using a boundary-anchored grid. *Nat. Neurosci.* 21 (2), 191–194. <https://doi.org/10.1038/s41593-017-0049-1>.
- Julian, J.B., Keinath, A.T., Marchette, S.A., Epstein, R.A., 2018b. The neurocognitive basis of spatial reorientation. *Curr. Biol.* 28 (17), R1059–R1073. <https://doi.org/10.1016/j.cub.2018.04.057>.
- Kaufman, L., Kramer, D.M., Crooks, L.E., Ortendahl, D.A., 1989. Measuring signal-to-noise ratios in MR imaging. *Radiology* 173 (1), 265–267. <https://doi.org/10.1148/radiology.173.1.2781018>.
- Khader, P., Burke, M., Bien, S., Ranganath, C., Rösler, F., 2005. Content-specific activation during associative long-term memory retrieval. *Neuroimage* 27 (4), 805–816. <https://doi.org/10.1016/j.neuroimage.2005.05.006>.
- Kim, M., Maguire, E.A., 2018. Hippocampus, retrosplenial and parahippocampal cortices encode multicompartment 3D space in a hierarchical manner. *Cerebral Cortex* (New York, N.Y. : 1991 28 (5), 1898–1909. <https://doi.org/10.1093/cercor/bhy054>.
- Kravitz, D.J., Saleem, K.S., Baker, C.L., Mishkin, M., 2011. A new neural framework for visuospatial processing. *Nat. Rev. Neurosci.* 12 (4), 217–230. <https://doi.org/10.1038/nrn3008>.
- Kriegeskorte, N., Mur, M., Bandettini, P., 2008. Representational similarity analysis - connecting the branches of systems neuroscience. *Front. Syst. Neurosci.* 2, 4. <https://doi.org/10.3389/neuro.06.004.2008>.
- Kunz, L., Brandt, A., Reinacher, P.C., Staresina, B.P., Reifensstein, E.T., Weidemann, C.T., Herweg, N.A., Patel, A., Tzitsiklis, M., Kempter, R., Kahana, M.J., Schulze-Bonhage, A., Jacobs, J., 2021. A neural code for egocentric spatial maps in the human medial temporal lobe. *Neuron* 109 (17), 2781–2796.e10. <https://doi.org/10.1016/j.neuron.2021.06.019>.
- Kurby, C.A., Zacks, J.M., 2008. Segmentation in the perception and memory of events. *Trends Cognit. Sci.* 12 (2), 72–79. <https://doi.org/10.1016/j.tics.2007.11.004>.
- Kyle, C.T., Stokes, J.D., Lieberman, J.S., Hassan, A.S., Ekstrom, A.D., 2015. Successful retrieval of competing spatial environments in humans involves hippocampal pattern separation mechanisms. *Elife* 4. <https://doi.org/10.7554/eLife.10499>.
- Lacy, J.W., Yassa, M.A., Stark, S.M., Muftuler, L.T., Stark, C.E.L., 2010. Distinct pattern separation related transfer functions in human CA3/dentate and CA1 revealed using high-resolution fMRI and variable mnemonic similarity. *Learn. Mem.* 18 (1), 15–18. <https://doi.org/10.1101/lm.197111>.
- Lee, S.A., Miller, J.F., Watrous, A.J., Sperling, M.R., Sharan, A., Worrell, G.A., Berry, B.M., Aronson, J.P., Davis, K.A., Gross, R.E., Lega, B., Sheth, S., Das, S.R., Stein, J.M., Gormiak, R., Rizzuto, D.S., Jacobs, J., 2018. Electrophysiological signatures of spatial boundaries in the human subiculum. *J. Neurosci. : Off. J. Soc. Neurosci.* 38 (13), 3265–3272. <https://doi.org/10.1523/JNEUROSCI.3216-17.2018>.
- Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., Burgess, N., 2009. Boundary vector cells in the subiculum of the hippocampal formation. *J. Neurosci.* 29 (31), 9771–9777.
- Lisman, J.E., Grace, A.A., 2005. The hippocampal-VTA loop: controlling the entry of information into long-term memory. *Neuron* 46 (5), 703–713. <https://doi.org/10.1016/j.neuron.2005.05.002>.
- Logie, M.R., Donaldson, D.I., 2021. Do doorways really matter: investigating memory benefits of event segmentation in a virtual learning environment. *Cognition* 209, 104578. <https://doi.org/10.1016/j.cognition.2020.104578>.
- Lu, Q., Hasson, U., Norman, K.A., 2022. A neural network model of when to retrieve and encode episodic memories. *Elife* 11. <https://doi.org/10.7554/eLife.74445>.
- Maguire, E.A., Burgess, N., Donnett, J.G., Frackowiak, R.S., Frith, C.D., O'Keefe, J., 1998. Knowing where and getting there: a human navigation network. *Science* 280 (5365), 921–924. <https://doi.org/10.1126/science.280.5365.921>.
- Marr, D., 1971. Simple memory: a theory for archicortex. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 262 (841), 23–81. <https://doi.org/10.1098/rstb.1971.0078>.
- Miller, J.F., Neufang, M., Solway, A., Brandt, A., Trippel, M., Mader, L., Hefft, S., Merkow, M., Polyn, S.M., Jacobs, J., Kahana, M.J., Schulze-Bonhage, A., 2013. Neural activity in human hippocampal formation reveals the spatial context of retrieved memories. *Science* (New York, N.Y.) 342 (6162), 1111–1114. <https://doi.org/10.1126/science.1244056>.
- Molitor, R.J., Sherrill, K.R., Morton, N.W., Miller, A.A., Preston, A.R., 2021. Memory reactivation during learning simultaneously promotes dentate gyrus/CA(2,3) pattern differentiation and CA(1) memory integration. *J. Neurosci. : Off. J. Soc. Neurosci.* 41 (4), 726–738. <https://doi.org/10.1523/JNEUROSCI.0394-20.2020>.
- Morgan, L.K., Macevoy, S.P., Aguirre, G.K., Epstein, R.A., 2011. Distances between real-world locations are represented in the human hippocampus. *J. Neurosci. : Off. J. Soc. Neurosci.* 31 (4), 1238–1245. <https://doi.org/10.1523/JNEUROSCI.4667-10.2011>.
- Mumford, J.A., Turner, B.O., Ashby, F.G., Poldrack, R.A., 2012. Deconvolving BOLD activation in event-related designs for multivoxel pattern classification analyses. *Neuroimage* 59 (3), 2636–2643. <https://doi.org/10.1016/j.neuroimage.2011.08.076>.
- Newton, D., Engquist, G., 1976. The perceptual organization of ongoing behavior. *J. Exp. Soc. Psychol.* 12, 436–450.
- Nielson, D.M., Smith, T.A., Sreekumar, V., Dennis, S., Sederberg, P.B., 2015. Human hippocampus represents space and time during retrieval of real-world memories. *Proc. Natl. Acad. Sci. U.S.A.* 112 (35), 11078–11083. <https://doi.org/10.1073/pnas.1507104112>.
- Norman, K.A., O'Reilly, R.C., 2003. Modeling hippocampal and neocortical contributions to recognition memory: a complementary-learning-systems approach. *Psychol. Rev.* 110 (4), 611–646. <https://doi.org/10.1037/0033-295X.110.4.611>.
- O'Keefe, J., Nadel, L., 1978. *The hippocampus as a Cognitive Map*. Oxford University Press.
- O'Mara, S.M., Sanchez-Vives, M.V., Brotons-Mas, J.R., O'Hare, E., 2009. Roles for the subiculum in spatial information processing, memory, motivation and the temporal control of behaviour. *Prog. Neuro-Psychopharmacol. Biol. Psychiatry* 33 (5), 782–790. <https://doi.org/10.1016/j.pnpbp.2009.03.040>.
- Peer, M., Epstein, R.A., 2021. The human brain uses spatial schemas to represent segmented environments. *Curr. Biol. : CB* 31 (21), 4677–4688.e8. <https://doi.org/10.1016/j.cub.2021.08.012>.
- Peer, M., Ron, Y., Monsa, R., Arzy, S., 2019. Processing of different spatial scales in the human brain. *Elife* 8. <https://doi.org/10.7554/eLife.47492>.
- Polyn, S.M., Norman, K.A., Kahana, M.J., 2009. A context maintenance and retrieval model of organizational processes in free recall. *Psychol. Rev.* 116 (1), 129–156. <https://doi.org/10.1037/a0014420>.
- Pu, Y., Kong, X.-Z., Ranganath, C., Melloni, L., 2022. Event boundaries shape temporal organization of memory by resetting temporal context. *Nat. Commun.* 13 (1), 622. <https://doi.org/10.1038/s41467-022-28216-9>.
- Radvansky, G.A., Copeland, D.E., 2006. Walking through doorways causes forgetting: situation models and experienced space. *Mem. Cognit.* 34 (5), 1150–1156. <https://doi.org/10.3758/bf03193261>.
- Radvansky, G.A., Krawietz, S.A., Tamplin, A.K., 2011. Walking through doorways causes forgetting: further explorations. *Q. J. Exp. Psychol.* 64 (8), 1632–1645. <https://doi.org/10.1080/17470218.2011.571267>, 2006.
- Ranganath, C., Ritchey, M., 2012. Two cortical systems for memory-guided behaviour. *Nat. Rev. Neurosci.* 13 (10), 713–726. <https://doi.org/10.1038/nrn3338>.
- Reagh, Z.M., Delarazan, A.I., Garber, A., Ranganath, C., 2020. Aging alters neural activity at event boundaries in the hippocampus and Posterior Medial network. *Nat. Commun.* 11 (1), 3980. <https://doi.org/10.1038/s41467-020-17713-4>.
- Ritchey, M., Montchal, M.E., Yonelinas, A.P., Ranganath, C., 2015. Delay-dependent contributions of medial temporal lobe regions to episodic memory retrieval. *Elife* 4. <https://doi.org/10.7554/eLife.05025>.
- Ritvo, V.J.H., Turk-Browne, N.B., Norman, K.A., 2019. Nonmonotonic plasticity: how memory retrieval drives learning. *Trends Cognit. Sci.* 23 (9), 726–742. <https://doi.org/10.1016/j.tics.2019.06.007>.
- Rosenbaum, R.S., Ziegler, M., Winocur, G., Grady, C.L., Moscovitch, M., 2004. I have often walked down this street before": fMRI studies on the hippocampus and other structures during mental navigation of an old environment. *Hippocampus* 14 (7), 826–835. <https://doi.org/10.1002/hipo.10218>.
- Rugg, M.D., Vilberg, K.L., 2013. Brain networks underlying episodic memory retrieval. *Curr. Opin. Neurobiol.* 23 (2), 255–260. <https://doi.org/10.1016/j.conb.2012.11.005>.
- Savelli, F., Yoganarasimha, D., Knierim, J.J., 2008. Influence of boundary removal on the spatial representations of the medial entorhinal cortex. *Hippocampus* 18 (12), 1270–1282. <https://doi.org/10.1002/hipo.20511>.
- Schapiro, A.C., Turk-Browne, N.B., Botvinick, M.M., Norman, K.A., 2017. Complementary learning systems within the hippocampus: a neural network modelling approach to reconciling episodic memory with statistical learning. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 372 (1711) <https://doi.org/10.1098/rstb.2016.0049>.
- Schwan, S., Garsoffky, B., Hesse, F.W., 2000. Do film cuts facilitate the perceptual and cognitive organization of activity sequences? *Mem. Cognit.* 28 (2), 214–223. <https://doi.org/10.3758/bf03213801>.
- Shine, J.P., Valdés-Herrera, J.P., Tempelmann, C., Wolbers, T., 2019. Evidence for allocentric boundary and goal direction information in the human entorhinal cortex and subiculum. *Nat. Commun.* 10 (1), 4004. <https://doi.org/10.1038/s41467-019-11802-9>.

- Smith, S.M., Vela, E., 2001. Environmental context-dependent memory: a review and meta-analysis. *Psychon. Bull. Rev.* 8 (2), 203–220. <https://doi.org/10.3758/bf03196157>.
- Solstad, T., Boccara, C.N., Kropff, E., Moser, M.-B., Moser, E.I., 2008. Representation of geometric borders in the entorhinal cortex. *Science* 322 (5909), 1865–1868.
- Spreng, R.N., Mar, R.A., Kim, A.S.N., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J. Cognit. Neurosci.* 21 (3), 489–510. <https://doi.org/10.1162/jocn.2008.21029>.
- Stangl, M., Topalovic, U., Inman, C.S., Hiller, S., Villaroman, D., Aghajan, Z.M., Christov-Moore, L., Hasulak, N.R., Rao, V.R., Halpern, C.H., Eliashiv, D., Fried, I., Suthana, N., 2021. Boundary-anchored neural mechanisms of location-encoding for self and others. *Nature* 589 (7842), 420–425. <https://doi.org/10.1038/s41586-020-03073-y>.
- Stemmers, B., Vicente-Grabovetsky, A., Barry, C., Smulders, P., Schröder, T.N., Burgess, N., Doeller, C.F., 2016. Hippocampal attractor dynamics predict memory-based decision making. *Curr. Biol.* : CB 26 (13), 1750–1757. <https://doi.org/10.1016/j.cub.2016.04.063>.
- Stevenson, R.F., Reagh, Z.M., Chun, A.P., Murray, E.A., Yassa, M.A., 2020. Pattern separation and source memory engage distinct hippocampal and neocortical regions during retrieval. *J. Neurosci.* : Off. J. Soc. Neurosci. 40 (4), 843–851. <https://doi.org/10.1523/JNEUROSCI.0564-19.2019>.
- Stokes, J., Kyle, C., Ekstrom, A.D., 2015. Complementary roles of human hippocampal subfields in differentiation and integration of spatial context. *J. Cognit. Neurosci.* 27 (3), 546–559. [https://doi.org/10.1162/jocn\\_a\\_00736](https://doi.org/10.1162/jocn_a_00736).
- Suzuki, W.A., Amaral, D.G., 2004. Functional neuroanatomy of the medial temporal lobe memory system. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior* 40 (1), 220–222. [https://doi.org/10.1016/s0010-9452\(08\)70958-4](https://doi.org/10.1016/s0010-9452(08)70958-4).
- Swallow, K.M., Barch, D.M., Head, D., Maley, C.J., Holder, D., Zacks, J.M., 2011. Changes in events alter how people remember recent information. *J. Cognit. Neurosci.* 23 (5), 1052–1064. <https://doi.org/10.1162/jocn.2010.21524>.
- Treves, A., Rolls, E.T., 1994. Computational analysis of the role of the hippocampus in memory. *Hippocampus* 4 (3), 374–391. <https://doi.org/10.1002/hipo.450040319>.
- Tse, D., Langston, R.F., Kakeyama, M., Bethus, I., Spooner, P.A., Wood, E.R., Witter, M.P., Morris, R.G.M., 2007. Schemas and memory consolidation. *Science (New York, N. Y.)* 316 (5821), 76–82. <https://doi.org/10.1126/science.1135935>.
- Tulving, E., 1972. In: Tulving, E., Donaldson, W. (Eds.), *Organization of Memory*, 381–403. Academic Press Inc.
- Tulving, E., Le Voi, M.E., Routh, D.A., Loftus, E., 1983. Euphoric processes in episodic memory [and discussion]. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 302 (1110), 361–371. <http://www.jstor.org/stable/2395999>.
- van Strien, N.M., Cappaert, N.L.M., Witter, M.P., 2009. The anatomy of memory: an interactive overview of the parahippocampal-hippocampal network. *Nat. Rev. Neurosci.* 10 (4), 272–282. <https://doi.org/10.1038/nrn2614>.
- Vinogradova, O.S., 2001. Hippocampus as comparator: role of the two input and two output systems of the hippocampus in selection and registration of information. *Hippocampus* 11 (5), 578–598. <https://doi.org/10.1002/hipo.1073>.
- Viskontas, I.V., Quiroga, R.Q., Fried, I., 2009. Human medial temporal lobe neurons respond preferentially to personally relevant images. *Proc. Natl. Acad. Sci. U. S. A.* 106 (50), 21329–21334. <https://doi.org/10.1073/pnas.0902319106>.
- Westfall, P., Young, S., 1993. *Resampling-based Multiple Testing: Examples and Methods for P-Value Adjustment*. Wiley.
- Witter, M.P., Groenewegen, H.J., Lopes da Silva, F.H., Lohman, A.H., 1989. Functional organization of the extrinsic and intrinsic circuitry of the parahippocampal region. *Prog. Neurobiol.* 33 (3), 161–253. [https://doi.org/10.1016/0301-0082\(89\)90009-9](https://doi.org/10.1016/0301-0082(89)90009-9).
- Yassa, M.A., Stark, C.E.L., 2011. Pattern separation in the hippocampus. *Trends Neurosci.* 34 (10), 515–525. <https://doi.org/10.1016/j.tins.2011.06.006>.
- Yonelinas, A.P., 2002. The nature of recollection and familiarity: a review of 30 Years of research. *J. Mem. Lang.* 46 (3), 441–517. <https://doi.org/10.1006/jmla.2002.2864>.
- Yoo, H., Bin, Umbach, G., Lega, B., 2022. Episodic boundary cells in human medial temporal lobe during the free recall task. *Hippocampus* 32 (7), 481–487. <https://doi.org/10.1002/hipo.23421>.
- Yushkevich, P.A., Wang, H., Pluta, J., Das, S.R., Craige, C., Avants, B.B., Weiner, M.W., Mueller, S., 2010. Nearly automatic segmentation of hippocampal subfields in in vivo focal T2-weighted MRI. *Neuroimage* 53 (4), 1208–1224. <https://doi.org/10.1016/j.neuroimage.2010.06.040>.
- Yushkevich, Paul A., Amaral, R.S.C., Augustinack, J.C., Bender, A.R., Bernstein, J.D., Boccardi, M., Bocchetta, M., Burggren, A.C., Carr, V.A., Chakravarty, M.M., Chételat, G., Daugherty, A.M., Davachi, L., Ding, S.-L., Ekstrom, A., Geerlings, M.I., Hassani, A., Huang, Y., Iglesias, J.E., et al., 2015a. Quantitative comparison of 21 protocols for labeling hippocampal subfields and parahippocampal subregions in in vivo MRI: towards a harmonized segmentation protocol. *Neuroimage* 111, 526–541. <https://doi.org/10.1016/j.neuroimage.2015.01.004>.
- Yushkevich, Paul A., Pluta, J.B., Wang, H., Xie, L., Ding, S.-L., Gertje, E.C., Mancuso, L., Klotz, D., Das, S.R., Wolk, D.A., 2015b. Automated volumetry and regional thickness analysis of hippocampal subfields and medial temporal cortical structures in mild cognitive impairment. *Hum. Brain Mapp.* 36 (1), 258–287. <https://doi.org/10.1002/hbm.22627>.
- Zacks, J.M., Speer, N.K., Reynolds, J.R., 2009. Segmentation in reading and film comprehension. *J. Exp. Psychol. Gen.* 138 (2), 307–327. <https://doi.org/10.1037/a0015305>.
- Zeidman, P., Maguire, E.A., 2016. Anterior hippocampus: the anatomy of perception, imagination and episodic memory. *Nat. Rev. Neurosci.* 17 (3), 173–182. <https://doi.org/10.1038/nrn.2015.24>.
- Zeidman, P., Lutti, A., Maguire, E.A., 2015. Investigating the functions of subregions within anterior hippocampus. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior* 73, 240–256. <https://doi.org/10.1016/j.cortex.2015.09.002>.
- Zeineh, M.M., Engel, S.A., Thompson, P.M., Bookheimer, S.Y., 2001. Unfolding the human hippocampus with high resolution structural and functional MRI. *Anat. Rec.* 265 (2), 111–120. <https://doi.org/10.1002/ar.1061>.
- Zeineh, M.M., Engel, S.A., Thompson, P.M., Bookheimer, S.Y., 2003. Dynamics of the hippocampus during encoding and retrieval of face-name pairs. *Science (New York, N.Y.)* 299 (5606), 577–580. <https://doi.org/10.1126/science.1077775>.
- Zheng, L., Gao, Z., McAvan, A.S., Isham, E.A., Ekstrom, A.D., 2021. Partially overlapping spatial environments trigger reinstatement in hippocampus and schema representations in prefrontal cortex. *Nat. Commun.* 12 (1), 6231. <https://doi.org/10.1038/s41467-021-26560-w>.
- Zheng, Y., Liu, X.L., Nishiyama, S., Ranganath, C., O'Reilly, R.C., 2021. Correcting the hebbian mistake: toward a fully error-driven Hippocampus. *bioRxiv*. <https://doi.org/10.1101/2021.10.29.466546>, 2021.10.29.466546.
- Zheng, J., Schjetnan, A.G.P., Yebra, M., Gomes, B.A., Mosher, C.P., Kalia, S.K., Valiante, T.A., Mamelak, A.N., Kreiman, G., Rutishauser, U., 2022. Neurons detect cognitive boundaries to structure episodic memories in humans. *Nat. Neurosci.* 25 (3), 358–368. <https://doi.org/10.1038/s41593-022-01020-w>.

## Further reading

- Ozdogan, T., Morris, G., 2012. *Evolution of change in the dynamics of coding in the hippocampus*. 8<sup>th</sup> FENS Forum of Neuroscience.