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Research report

Distinct regions of the hippocampus are associated with memory for different spatial locations

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A B S T R A C T

In the present functional magnetic resonance imaging (fMRI) study, we aimed to evaluate whether distinct regions of the hippocampus were associated with spatial memory for items presented in different locations of the visual field. In Experiment 1, during the study phase, participants viewed abstract shapes in the left or right visual field while maintaining central fixation. At test, old shapes were presented at fixation and participants classified each shape as previously in the "left" or "right" visual field followed by an "unsure"-"sure"-"very sure" confidence rating. Accurate spatial memory for shapes in the left visual field was isolated by contrasting accurate versus inaccurate spatial location responses. This contrast produced one hippocampal activation in which the interaction between item type and accuracy was significant. The analogous contrast for right visual field shapes did not produce activity in the hippocampus; however, the contrast of high confidence versus low confidence right-hits produced one hippocampal activation in which the interaction between item type and confidence was significant. In Experiment 2, the same paradigm was used but shapes were presented in each quadrant of the visual field during the study phase. Accurate memory for shapes in each quadrant, exclusively masked by accurate memory for shapes in the other quadrants, produced a distinct activation in the hippocampus. A multi-voxel pattern analysis (MVPA) of hippocampal activity revealed a significant correlation between behavioral spatial location accuracy and hippocampal MVPA accuracy across participants. The findings of both experiments indicate that distinct hippocampal regions are associated with memory for different visual field locations.

1. Introduction

It has long been known that hippocampal place cells in rodents fire when an animal is in a particular location in space (O'Keefe and Dostrovsky, 1971). Hippocampal place cells have also been identified in other animals, such as bats and primates (for a review, see Hartley et al., 2014). For example, single-cell recording from the monkey hippocampus has demonstrated that there are place cells that are activated by both specific locations in an experimental room and specific locations on a computer screen (Matsumura et al., 1999). Such findings in animals have given rise to the cognitive map theory of hippocampal function, where distinct hippocampal regions are associated with different spatial locations (O'Keefe and Nadel, 1978). Functional magnetic resonance imaging (fMRI) studies with humans have also suggested that the hippocampus is involved during spatial navigation (Maguire et al., 1998; Burgess et al., 2002; Ekstrom et al., 2003; Maguire et al., 2006; Zhang and Ekstrom, 2013; Howard et al., 2014). Additionally, single-cell recording from the human hippocampus has revealed that place cells are active during virtual navigation tasks (Ekstrom et al., 2003; Miller et al., 2013).

Although the evidence from fMRI studies and single-cell recording studies in humans has consistently shown that distinct hippocampal regions are associated with different spatial locations (in line with the cognitive map theory), these studies employed spatial navigation tasks which utilized maps, mazes, or movies of real-world environments. Such spatial navigation tasks involve many cognitive processes in addition to spatial memory, such as the perceptual processing of sensory cues (e.g., environmental cues and self-motion cues) and several executive mechanisms (e.g., setting navigational goals, route planning, and maintaining spatial representations; McNamara et al., 2008; Wolbers and Hegarty,

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2010; Rodriguez, 2011; Chersi and Burgess, 2015; Spiers and Barry, 2015; Wolbers, 2015). These cognitive processes are further involved in regulating navigational spatial computations such as path integration, spatial updating, and wayfinding, and, critically, they are associated with brain regions that extend beyond the hippocampus, such as the striatum, the precuneus, and the entorhinal cortex (for a review, see Wolbers, 2015). Thus, the navigation tasks used in previous studies with humans have confounded spatial memory with other spatial computations. Of importance, there has been no evidence that different regions of the human hippocampus code for different spatial locations during a task that has only involved spatial memory.

In the current fMRI study, we aimed to evaluate whether distinct regions of the human hippocampus were involved with memory for different spatial locations by utilizing paradigms that isolated visual spatial memory (to eliminate the confounds associated with spatial navigation). In Experiment 1, we evaluated whether the hippocampus was differentially associated with memory for items presented along the horizontal meridian in the left visual field or the right visual field. During the study phase, abstract shapes were presented to the left or right of fixation (Fig. 1, left). During the test phase, old shapes were presented at fixation and participants classified each shape as previously in the "left" or "right" visual field (Fig. 1, right). Experiment 1 was a re-analysis of a dataset from a previous study where we found that the magnitudes of activity in the anterior prefrontal cortex and the hippocampus were negatively correlated during false memories (Jeye et al., 2017). The current study extended our prior findings as only the present analysis assessed whether there were differential spatial location effects in the hippocampus. In Experiment 2, we evaluated whether the hippocampus was differentially associated with memory for items presented in each quadrant of the visual field.

Our analytic plan consisted of multiple tests to uncover distinct regions of the hippocampus associated with memory for different spatial locations. First, we attempted to isolate hippocampal activity associated with accurate memory for each spatial location by comparing correct spatial location responses (hits) with incorrect spatial location responses (misses). If either of the spatial locations were associated with null hippocampal activity, to increase power, we compared all correct spatial location responses and all incorrect spatial location responses. Finally, if both of the previous analyses were associated with null hippocampal activity (for either spatial location), we compared high confidence hits and low confidence hits for each spatial location.

2. Results

2.1. Experiment 1

Spatial location accuracy did not differ between shapes previously presented in the left visual field (75.5%, chance = 50%) and shapes previously presented in the right visual field (78.6%; $t(15) < 1$). The present analysis focused on hippocampal activity associated with spatial memory during the retrieval phase.

Hippocampal activity associated with accurate spatial memory for shapes in the left visual field was isolated by contrasting correct spatial location responses (left-hits) with incorrect spatial location responses (left-misses; i.e., "left"/left > "right"/left). This contrast produced two activations in the body of the left hippocampus (Fig. 2, top left, coordinates, $x = -27$, $y = -14$, $z = -15$, size = 54 mm^3; bottom left, $x = -24$, $y = -19$, $z = -11$, size = 27 mm^3; see Supplementary Material Figs. S1 and S2 for activations projected on individual participant anatomic images). Event-related activation magnitudes were extracted from both hippocampal activations. In the more anterior hippocampal activation (Fig. 2, top right), the interaction between item location (left, right) and accuracy (hits, misses) was not significant ($t(15) < 1$). Of importance, in the more posterior hippocampal activation (Fig. 2, bottom right), there was a significant interaction between item location and accuracy ($t(15) = 1.90$, $p < .05$). Hippocampal activity associated with accurate spatial memory for shapes in the right visual field was isolated by contrasting right-hits and right-misses (i.e., "right"/right > "left"/right). Unexpectedly, this contrast did not produce any activations in the hippocampus. This null finding is consistent with the event-related activation profiles corresponding to the previous contrast (Fig. 2, right), as the activations associated with right-hits were more negative in magnitude than those associated with right-misses. The results thus far suggest that the hippocampus is preferentially associated with spatial memory for items in the left visual field.

We conducted additional analyses in an effort to uncover hippocampal activity associated with memory for shapes in the right visual field. To increase power, all correct spatial location responses were contrasted with all incorrect spatial location responses (i.e., all-hits > all-misses). At a threshold of $p < .001$, uncorrected, this contrast produced two activations in the hippocampus (Supplementary Material Fig. S3, top left, coordinates $x = -24$, $y = -16$, $z = -14$, size = 54 mm^3; bottom left, coordinates $x = 18$, $y = -34$, $z = 4$, size = 27 mm^3). In the more anterior hippocampal activation (Supplementary Material Fig. S3, top right),

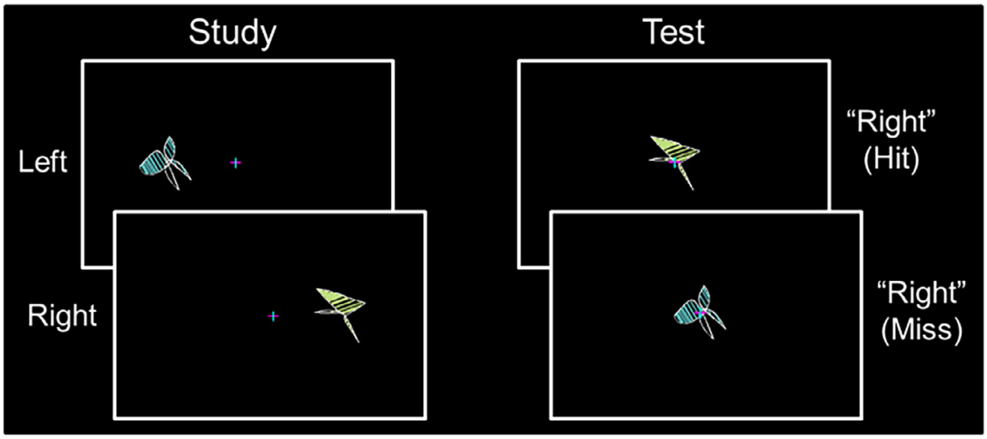

Fig. 1. Left, during the study phase of Experiment 1, abstract shapes were presented in the left or right visual field. Right, during the test phase, shapes were presented at fixation and participants classified each shape as previously on the "left" or "right" followed by an "unsure"-"sure"- "very sure" confidence response. Example spatial location responses are shown to the right (with response types in parenthesis).