# Gaze-centered spatial representations in human hippocampus

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**Abstract:**

**As we move our eyes around the world, we are able to integrate visual input and achieve a stable visual percept across eye movements. However, previous studies have found that our visual system, from primary visual cortex to higher level visual regions, represents object locations in natively retinotopic (gaze-centered) but not spatiotopic (gaze-independent) coordinates. Is spatiotopic information represented elsewhere in the brain, or might we achieve gaze-independent behavior via other means? Two key properties of the hippocampus make it an ideal candidate area to search for spatiotopic information: its responsiveness to visual information and its role in other types of complex spatial processing. In this study, we manipulated fixation and stimulus locations in an object perception task and used functional fMRI to record participants' brain activity. Here, we use correlation-based multi-voxel pattern analysis (MVPA) and representational similarity analysis (RSA) to explore the representation of object location and investigate a potential role for the human hippocampus in visual stability. We found significant retinotopic instead of spatiotopic information not only in LOC and PPA (consistent with prior findings), but also in hippocampus. These results reveal that hippocampus also encodes gaze-centered spatial information, extending findings that the native coordinate system of vision might be retinotopic throughout the brain, with other mechanisms responsible for achieving gaze-independent behavior.**

**Keywords: spatial reference frames; retinotopic; spatiotopic; MVPA; RSA; visual perception**

## Introduction

As we move our eyes around the world, we feel as though we are able to piece together the visual snapshots we get with each glance into a complete picture of the world. To do this, our brains need to somehow integrate the object location from retinotopic (gaze-centered) coordinates to spatiotopic (gaze-independent) coordinates. Despite relatively successful spatiotopic behavior, however, previous work has shown evidence of retinotopic but not spatiotopic neural representations, not only in early visual areas (Gardner et al., 2008; Golomb and Kanwisher, 2012), but also in later visual areas, including category-selective ventral regions and parietal regions (Golomb & Kanwisher, 2012). One brain region not previously explored is the hippocampus, which has recently gained traction as an area containing visual representations (Lee et al., 2012, Turk-Browne, 2019; Silson et al., 2021). Might the hippocampus be involved in object location coding and contain the elusive spatiotopic representations? On the one hand, hippocampus shares connectivity with visual regions which have gaze-centered representation (Knapen, 2020). One the other hand, hippocampus is downstream of the entorhinal cortex which contains grid-cells encoding gaze-independent spatial information for navigation (Haft et al., 2005).

In this study, we manipulated fixation position and stimulus location to differentiate gaze-centered vs. gaze-independent visual processing in two fMRI experiments. We used both correlation-based multi-voxel pattern analysis (MVPA) (Haxby et al., 2001) and representational similarity analysis (RSA) (Kriegeskorte et al., 2008) to test whether hippocampus contains information about the location of visual stimuli and investigate if the encoding format of hippocampus is retinotopic and/or spatiotopic across gaze changes.

## Methods

Stimuli were presented in a blocked fMRI design. Each 16s block contained a sequence of 20 images (Expt 1: drawn from a set of black-and-white objects or scenes; Expt 2: drawn from a set of colored real-world objects). For both experiments, participants were asked to do a one-back task. In Expt 1, there were two possible fixation locations, and the stimulus was shown on the

left or right of the fixation (Fig 1). In Expt 2, there were four possible stimulus locations (left top, left bottom, right top and right bottom) around each fixation (Fig 2).

Subjects were scanned in 8 task runs consisting of 16 blocks each, as well as 3 localizer runs on a Siemens 3T Prisma scanner, with a 32-channel coil and EPI sequences with the following parameters: 2.5s TR, 2.8ms TE, 2x2x2 $mm^3$ resolution, 10% gap, slices aligned perpendicular to the main axis of the hippocampus. This gave us coverage of anterior occipital, posterior temporal, posterior parietal cortex and hippocampus. Standard preprocessing steps were performed in BrainVoyager with Freesurfer used for hippocampus localization.

In Expt 1, we conducted split-half MVPA. We created correlation matrices by splitting data into odd and even runs and averaging responses for each voxel in each condition, and then calculated correlation differences (fisher-z transformed) for different types of spatial information (within-fixation location, across-fixation retinotopic, across-fixation spatiotopic). In Expt 2, the more complex design helped us further distinguish different location conditions. We created representational dissimilarity matrices (RDMs) by extracting the across-fixation cells, and then calculated the representational similarity between three fMRI ROIs (LOC, PPA, hippocampus) and three models (precise retinotopic, coarse hemifield, spatiotopic; Fig 2B). We also conducted a general linear model (GLM)-based RSA (Proklova et al., 2016, 2019; Kaiser et al., 2019) and partitioning analysis (Legendre, 2008; Bonner & Epstein, 2018; Dwivedi et al., 2021) to obtain unique and shared variance of retinotopic and hemifield (Fig 3). P-values were computed via permutation tests.

## Results

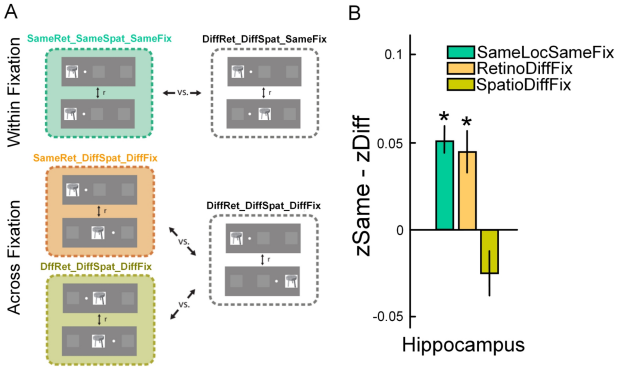


Figure 1: (A) MVPA logic and (B) results for Expt 1.

In Expt 1, we found significant within-fixation location information and across-fixation retinotopic information, but not across-fixation spatiotopic information, in hippocampus (Fig 1B). Here the design did not allow us to differentiate finer retinotopic information from coarser hemifield information, so we conducted Expt 2 to replicate and differentiate this gaze-centered pattern.

In Expt 2, RSA revealed significant representational similarity to both gaze-centered models (retinotopic and hemifield) in all three ROIs. Consistent with Expt 1, there was no significant representational similarity to the spatiotopic model (Figure 2C). Variance partitioning

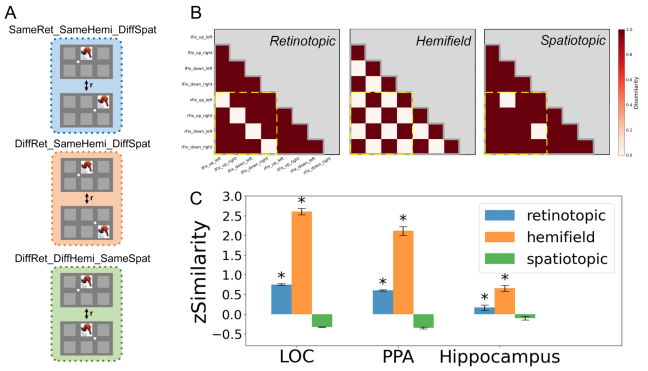


Figure 2: (A) Different experimental conditions, (B) model RDMs and (C) RSA results for Expt 2.

analysis showed that gaze-centered location encoding in LOC, PPA, and hippocampus included contributions of retinotopic and hemifield information, with additional shared variance in LOC and PPA (Fig 3).

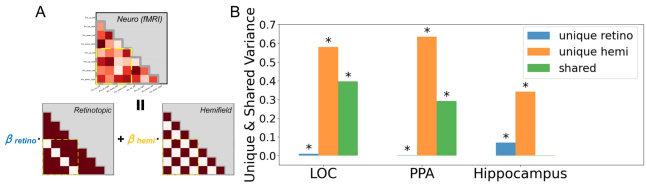


Figure 3: (A) GLM-based RSA and (B) variance partitioning analysis results for Expt 2.

## Conclusion

Human hippocampus contains visual representations of object location in gaze-centered coordinates. Combining both MVPA and RSA results, we found that hippocampus encodes gaze-centered but not gaze-independent object location information across different fixation locations, which is consistent with patterns in human visual cortex. Our results extend findings that the native coordinate system of vision might be retinotopic throughout the brain. Moreover, we find that while gaze-centered locations are primarily consistent with coarse hemifield information, there is a small additional contribution of finer retinotopic information.

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