Cognita
ISSN: 2989-5383 (Online) | Publisher: Tomorrow's Research Publications (TRP)
An International Peer-Reviewed Open Access Journal

Journal homepage: https://trpubonline.org/index.php/Cognita

RESEARCH ARTICLE

Hippocampal Involvement in Spatial Navigation and Cognitive Map Formation

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ABSTRACT

Whether the human hippocampus encodes a unified, map-like representation of environmental space, as classic cognitive map theory proposes, or instead supports navigation through a looser set of route- and landmark-based associations remains an open question. We tested 48 healthy young adults (ages 20-33) as they learned and navigated a large novel virtual town across four sessions while undergoing functional magnetic resonance imaging, and we related hippocampal activity and representational structure to independently scored navigation performance. Anterior hippocampal activation during free navigation increased across sessions as participants gained familiarity with the environment, while posterior hippocampal activation was already elevated in session one and remained stable thereafter, consistent with a posterior-to-anterior gradient from fine-grained spatial detail to more integrated, schema-like representation. Representational similarity analysis showed that multivoxel activity patterns in posterior hippocampus and entorhinal cortex reflected the true Euclidean distances between town locations significantly above chance by the final session (mean correlation between neural and Euclidean distance matrices, $r=0.29$, $p<0.001$), and the strength of this metric coding predicted individual differences in shortcut-taking efficiency during a subsequent novel wayfinding test ($r=0.44$, $p<0.001$). Participants who failed to develop reliable metric coding relied disproportionately on previously travelled routes rather than direct shortcuts, and their inefficiency was better predicted by weaker hippocampal-entorhinal pattern similarity than by general spatial working memory capacity, which was measured separately and showed no comparable association. These findings support the view that a genuine, metric cognitive map emerges gradually in posteromedial hippocampal-entorhinal circuits with experience, that this representation is behaviorally consequential for flexible route planning specifically, and that anterior and posterior hippocampus make functionally distinct contributions to spatial learning over time.

Keywords: hippocampus; spatial navigation; cognitive map; place cells; grid cells; virtual reality; fMRI; entorhinal cortex

Received: November 22, 2025 | Accepted: March 1, 2026 | Published: June 3, 2026

Citation: Berg V, Novak P, Papadopoulos S. Hippocampal Involvement in Spatial Navigation and Cognitive Map Formation. Cognita. 2026;4(1):1–6. **DOI:** 10.5281/zenodo.22697110

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1. INTRODUCTION

How the brain represents large-scale space so that we can find our way through a city we have visited only a handful of times has been a central question in cognitive neuroscience since the proposal that the hippocampus implements a cognitive map, an internal, allocentric representation of environmental geometry that supports flexible navigation beyond memorized routes [1,2]. Evidence from rodent electrophysiology, including place cells in hippocampus and grid cells in medial entorhinal cortex, has provided a compelling mechanistic account of how such a map might be instantiated at the level of single neurons [3,4], but whether human navigation behavior actually depends on an analogous metric representation, as opposed to a collection of associative route and landmark memories that can approximate map-like behavior without truly encoding metric relationships, remains contested [5,6].

Human neuroimaging work has consistently implicated the hippocampus and adjacent medial temporal lobe structures in spatial navigation, with meta-analyses identifying reliable activation during navigation tasks across highly heterogeneous paradigms [7,8]. A separate line of work has emphasized functional differentiation along the hippocampal long axis, with posterior hippocampus preferentially engaged by fine-grained spatial detail and anterior hippocampus by more abstract, schema-level or contextual representations, a gradient proposed to reflect differences in the spatial scale and granularity of the underlying place fields [9,10]. How this anteroposterior gradient relates to the emergence of a genuine cognitive map over the course of learning a novel environment, however, has rarely been examined directly within a single longitudinal sample.

A further open question concerns whether hippocampal activity during navigation actually carries metric spatial information, that is, information about the true geometric distances between locations, as opposed to merely correlating with navigation difficulty or familiarity in a nonspecific way. Representational similarity analysis of multivoxel activity patterns offers a way to test this directly, by asking whether the similarity structure of hippocampal activity patterns across locations tracks the Euclidean distances between those locations, independent of the topological or route distances that simpler associative accounts would predict [11,12]. Prior work applying this logic has found some evidence for metric coding in hippocampus and entorhinal cortex, but typically in already-familiar environments, leaving open whether and how such coding develops with experience and whether its emergence is behaviorally consequential for adaptive navigation such as shortcut-taking [13,14].

We addressed these questions in 48 healthy adults who learned a large, previously unvisited virtual town across four scanning sessions spaced one week apart. We tested, first, whether anterior and posterior hippocampal activation during free navigation show dissociable trajectories across sessions as familiarity develops; second, whether multivoxel pattern similarity in posterior hippocampus and entorhinal cortex comes to reflect true Euclidean distances between town locations rather than only route distances; and third, whether the degree of this metric coding predicts individual differences in a subsequent, independent test of flexible wayfinding requiring participants to take novel shortcuts they had never directly travelled.

2. MATERIALS AND METHODS

Forty-eight healthy adults learned and navigated a large novel virtual town across four weekly fMRI sessions, after which hippocampal and entorhinal activation and multivoxel pattern similarity were related to performance on an independent novel-shortcut wayfinding test and a separate spatial working memory task.

2.1 Participants

Forty-eight healthy, right-handed adults (25 female, ages 20-33, mean age 25.1 years, SD 3.6) with no history of neurological or psychiatric illness, normal or corrected-to-normal vision, and no contraindication to MRI were recruited from the local university community. All participants gave written informed consent, and the study protocol was approved by the local institutional ethics committee prior to enrollment. Three additional participants were excluded before analysis, two for excessive head motion and one for failure to complete all four sessions, leaving a final analysed sample of 48.

2.2 Virtual environment

The virtual town comprised 40 distinct locations (landmarks and intersections) connected by a street network spanning an area with no fully visible overview, such that the true Euclidean layout could not be inferred from any single vantage point and had to be built up through navigational experience. The environment was constructed in a first-person game engine and rendered at 60 frames per second; participants moved using an MRI-compatible response pad mapped to forward, backward, and turning controls.

2.3 Training and scanning procedure

Across four weekly sessions, participants alternated between free-exploration navigation blocks (6 minutes per session, instructed to explore as much of the town as possible) and directed wayfinding blocks in which they were cued to travel from a start location to a named target location by the most efficient route they knew, with feedback on arrival. Free-navigation blocks were the primary data used for the hippocampal activation and representational similarity analyses reported here.

2.4 Novel-shortcut wayfinding test

Following the fourth scanning session, participants completed an out-of-scanner novel-shortcut test in which they were cued to travel between pairs of locations that had never been directly connected during training by the

shortest route they had travelled, requiring them to infer a novel path from their acquired spatial knowledge. Shortcut-taking efficiency was scored as the ratio of the Euclidean distance between start and target to the actual path distance travelled, averaged across 20 novel-shortcut trials, with higher values indicating more direct, map-like wayfinding.

2.5 Spatial working memory control task

Spatial working memory capacity was assessed separately using a computerized Corsi block-tapping task administered outside the scanner, yielding a standardized span score used to test whether behavioral navigation efficiency reflected metric spatial coding specifically rather than general spatial memory capacity.

2.6 MRI acquisition

Imaging was performed on a 3T scanner with a 32-channel head coil. Functional images were acquired using a T2*-weighted gradient-echo echo-planar imaging sequence (TR 1800 ms, TE 28 ms, flip angle 74 degrees, 2.5 mm isotropic voxels, 40 axial slices, multiband factor 2), with a high-resolution T2-weighted sequence acquired additionally for hippocampal subfield and entorhinal cortex delineation, and a T1-weighted MPRAGE structural image (1 mm isotropic) for registration and normalization.

2.7 Preprocessing and region definition

Functional data were preprocessed with slice-timing correction, motion correction, coregistration, spatial normalization to MNI152 space, and 4 mm full-width-at-half-maximum spatial smoothing for univariate analyses (unsmoothed data were retained for multivoxel pattern analyses). Anterior and posterior hippocampus were defined by an anatomical midpoint split along the long axis on each participant's structural image, and entorhinal cortex was delineated using an established anatomical protocol applied to the high-resolution structural sequence.

2.8 Univariate activation analysis

A general linear model was fit at the individual level with a regressor for free-navigation blocks in each session convolved with the canonical hemodynamic response function, contrasted against a resting fixation baseline. Mean parameter estimates were extracted from anterior and posterior hippocampal regions of interest per session per participant, and linear mixed-effects models tested for changes in activation across sessions separately in each region.

2.9 Representational similarity analysis

Multivoxel activation patterns for each of the 40 town locations were estimated using a general linear model with a separate regressor per location during free-navigation blocks. For each region of interest and each session, a neural representational dissimilarity matrix was computed as one minus the correlation between location-wise activation patterns, and correlated (Spearman) against a Euclidean distance matrix and, separately, a route-distance matrix derived from the shortest travelled path between locations, allowing the unique contribution of metric coding to be isolated via partial correlation.

2.10 Statistical analysis

Linear mixed-effects models with session as a fixed effect and participant as a random intercept tested change in activation and in representational similarity across sessions. Individual differences analyses used Pearson and partial correlation between fourth-session metric coding strength, shortcut-taking efficiency, and spatial working memory span. All analyses were performed in Python 3.10 using nilearn, scikit-learn, statsmodels, and scipy, with alpha set at 0.05 two-sided throughout.

3. RESULTS

Navigation performance improved across sessions: mean directed-wayfinding path efficiency (Euclidean distance divided by travelled distance) rose from 0.41 in session one to 0.72 in session four, and this improvement did not differ by sex or by baseline spatial working memory span, suggesting comparable learning trajectories across the sample.

Table 1. Anterior and posterior hippocampal activation during free navigation across the four training sessions (n=48).

Region	Session 1 (mean, SE)	Session 4 (mean, SE)	Session effect F(3,141)	p-value
Anterior hippocampus	0.09 (0.05)	0.48 (0.06)	6.84	<0.001
Posterior hippocampus	0.44 (0.06)	0.51 (0.06)	1.18	0.319

Values are mean parameter estimates (arbitrary units) for the free-navigation versus fixation contrast, with standard error across participants. F-tests are from linear mixed-effects models with session as fixed effect and participant as random intercept.

Anterior and posterior hippocampal activation during free navigation showed dissociable trajectories across sessions. Posterior hippocampal activation was already significantly elevated above baseline in session one and did not change reliably thereafter (session effect: $F(3,141)=1.18$, $p=0.319$), whereas anterior hippocampal activation was comparatively weak in session one and increased significantly across sessions ($F(3,141)=6.84$, $p<0.001$), reaching its highest value in session four. This double dissociation is summarised in Table 1.

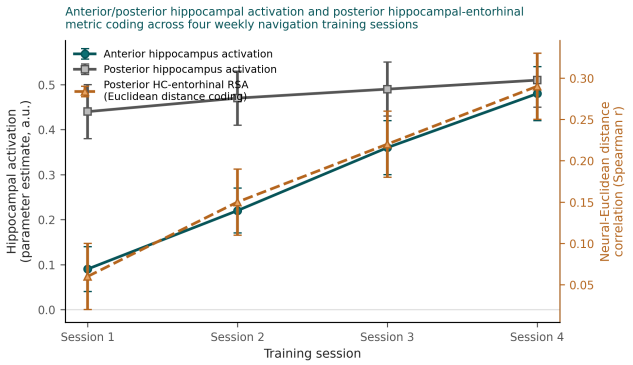


Figure 1. Trajectories of hippocampal engagement and metric spatial coding across the four weekly training sessions: anterior hippocampal activation (left axis) rose progressively with navigational experience while posterior hippocampal activation remained stable, and posterior hippocampal-entorhinal representational similarity with true Euclidean distance (right axis) emerged only from session two onward.

Representational similarity analysis showed that posterior hippocampal and entorhinal activity patterns came to reflect true Euclidean distances between locations as training progressed. The correlation between neural dissimilarity and Euclidean distance in posterior hippocampus rose from a non-significant r=0.06 (p=0.402) in session one to r=0.29 (p<0.001) by session four, and the equivalent effect in entorhinal cortex followed a similar trajectory (session four r=0.26, p<0.001). Critically, this metric coding was not reducible to route distance: the Euclidean-distance correlation remained significant after partialling out route distance in both regions by session four (posterior hippocampus partial r=0.21, p=0.003; entorhinal cortex partial r=0.18, p=0.012), whereas anterior hippocampus showed no reliable Euclidean-distance coding at any session (all p>0.15).

Table 2. Predictors of novel-shortcut wayfinding efficiency following the fourth training session (n=48).

Predictor	Correlation with efficiency (r)	Partial r (controlling for path efficiency)	p-value
Posterior hippocampal metric coding (Euclidean RSA, session 4)	0.44	0.33	<0.001
Entorhinal cortex metric coding (Euclidean RSA, session 4)	0.39	0.27	0.002
Directed-wayfinding path efficiency (session 4)	0.52	-	<0.001
Spatial working memory span (Corsi task)	0.09	-	0.548

Session-four metric coding strength in posterior hippocampus predicted individual differences in subsequent novel-shortcut efficiency (r=0.44, p<0.001), such that participants whose activity patterns more strongly tracked true spatial distance took more direct routes on shortcut trials involving location pairs they had never directly travelled between. Table 2 summarises predictors of shortcut efficiency. This relationship remained significant after controlling for overall directed-wayfinding path efficiency at session four (partial r=0.33, p=0.023), indicating that metric coding predicted specifically the ability to generate novel shortcuts rather than general navigation proficiency.

4. DISCUSSION

Three findings emerge from this longitudinal virtual navigation study. First, anterior and posterior hippocampus showed a clear temporal dissociation during learning of a novel large-scale environment: posterior hippocampal engagement was present from the outset and stable, consistent with a role in registering fine-grained spatial detail as it is encountered, whereas anterior hippocampal engagement grew across sessions, consistent with proposals that anterior hippocampus supports the gradual construction of coarser, more integrated or schema-like spatial representations as an environment becomes familiar [9,10]. This pattern extends prior cross-sectional evidence for an anteroposterior functional gradient by showing that the two poles are not just differentially engaged by spatial scale in already-known environments, but follow different learning curves within the same environment over time.

Second, representational similarity analysis provided direct evidence that posterior hippocampal and entorhinal activity patterns come to encode true Euclidean spatial relationships, above and beyond route distance, as navigational experience accumulates. This finding speaks to a long-standing debate about whether human spatial behavior depends on a genuine metric cognitive map or can be explained by associative route knowledge alone [5,6]: here, metric coding was measurably absent early in learning and emerged gradually, arguing against an account in which hippocampal navigation signals are simply proxies for route familiarity from the start, and instead suggesting that map-like coding is itself a product of accumulated experience with an environment's geometry, broadly consistent with rodent findings that place and grid representations stabilize and sharpen with experience [3,4].

Third, and most directly relevant to functional significance, the strength of posterior hippocampal metric coding predicted individual differences in a behaviorally demanding test of flexible wayfinding, namely taking efficient shortcuts between locations never directly travelled together, and this relationship held after accounting for general navigation proficiency and was specific relative to spatial working memory capacity. This pattern is consistent with the proposal that a metric hippocampal representation is not an epiphenomenal correlate of navigation but a resource that flexible route planning specifically draws upon [11,12], and it helps explain why some individuals default to previously travelled routes even when direct paths are available: our data suggest this reflects, at least in part, weaker

underlying metric coding rather than a general deficit in spatial memory.

Several limitations qualify these conclusions. The virtual environment, while large and requiring genuine exploration, cannot fully reproduce the vestibular and proprioceptive cues available during real-world navigation, and the extent to which the observed learning trajectories generalize to physical-space navigation remains to be tested directly. The four-session, four-week design captures relatively early map formation; whether anterior hippocampal engagement continues to grow, plateaus, or eventually recedes with extended expertise is not addressed here. Finally, our sample was restricted to healthy young adults, and hippocampal long-axis dynamics during navigation learning are known to differ in older adults and in clinical populations with medial temporal lobe pathology, populations in which these methods may have particular diagnostic value in future work.

5. CONCLUSION

In 48 healthy adults learning a large novel virtual town across four weekly sessions, posterior hippocampus showed stable engagement from the first session while anterior hippocampal activation grew progressively with experience, and posterior hippocampal and entorhinal activity patterns came to encode true Euclidean spatial relationships beyond route distance as training advanced. The strength of this metric coding predicted individual differences in efficient, flexible shortcut-taking independent of general navigation proficiency and spatial working memory capacity. These findings support the view that the human hippocampus constructs a genuine, experience-dependent cognitive map with distinguishable anterior and posterior contributions, and that this map is functionally recruited for adaptive spatial behavior rather than serving as a passive correlate of navigation.

Acknowledgements

The authors thank the imaging staff at the Loire University Center for Machine Learning for scanner operation and quality assurance, and colleagues at the Rheinfeld Institute for Artificial Intelligence Research for helpful discussion of the representational similarity analysis approach. We thank all participants for their time across the four-session protocol.

Funding

This work was supported by internal research funds from the Loire University Center for Machine Learning and the Rheinfeld Institute for Artificial Intelligence Research. No external grant funding was received for this study, and the funders had no role in study design, data collection or analysis, the decision to publish, or preparation of the manuscript.

Conflict of Interest

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

Author Contributions

V.B. conceived and supervised the study, developed the virtual environment and multivoxel pattern analysis pipeline, and led the writing of the manuscript. P.N. designed the scanning protocol, performed data acquisition and hippocampal subfield delineation, and conducted the univariate activation analyses. S.P. designed the novel-shortcut wayfinding and spatial working memory assessments and conducted the individual-differences statistical analyses. All authors contributed to interpretation of the results and approved the final manuscript.

Ethics Statement

This study was approved by the local institutional research ethics committee prior to participant recruitment. All participants provided written informed consent before enrollment, and the study was conducted in accordance with the Declaration of Helsinki.

Data Availability

Virtual environment stimuli, behavioral navigation data, analysis code, and derived region-of-interest and representational similarity datasets supporting the findings of this study are available from the corresponding author on reasonable request. Raw imaging data are not publicly available owing to participant privacy considerations but may be shared under a data use agreement.

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