Repetition Suppression Reveals Cue-specific Spatial Representations for Landmarks and Self-motion Cues in Human Retrosplenial Cortex

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Title Page

1. Manuscript Title (50 word maximum)

Repetition Suppression Reveals Cue-specific Spatial Representations for Landmarks and Self-motion Cues in Human Retrosplenial Cortex

2. Abbreviated Title (50 character maximum)

Cue-specific positional coding in retrosplenial cortex

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Abstract

The efficient use of various spatial cues within a setting is crucial for successful navigation. Two fundamental forms of spatial navigation, landmark-based and self-motion-based, engage distinct cognitive mechanisms. The question of whether these modes invoke shared or separate spatial representations in the brain remains unresolved. While non-human animal studies have yielded inconsistent results, human investigation is limited. In our previous work (Chen et al., 2019), we introduced a novel spatial navigation paradigm utilizing ultra-high field fMRI to explore neural coding of positional information. We found that different entorhinal subregions in the right hemisphere encode positional information for landmarks and self-motion cues. The present study tested the generalizability of our previous finding with a modified navigation paradigm. Although we did not replicate our previous finding in the entorhinal cortex, we identified adaptation-based allocentric positional codes for both cue types in the retrosplenial cortex, which were not confounded by the path to the spatial location. However, the multi-voxel patterns of these spatial codes differed between the cue types, suggesting cue-specific positional coding. The parahippocampal cortex exhibited positional coding for self-motion cues, which was not dissociable from path length. Finally, the brain regions involved in successful navigation differed from our previous study, indicating overall distinct neural mechanisms recruited in our two studies. Taken together, the current findings demonstrate cue-specific allocentric positional coding in the human retrosplenial cortex in the same navigation task for the first time, and that spatial representations in the brain are contingent on specific experimental conditions.
**Significance Statement**

Effective navigation depends on efficient utilization of various spatial cues within an environment. Understanding how neural representations derived from distinct spatial cues relate — whether they are cue-specific or cue-independent — is paramount. The current study employed desktop virtual reality, ultra-high-field fMRI, and a novel repetition suppression paradigm that contrasted landmarks and self-motion cues. While not replicating our previous finding of positional coding in the entorhinal cortex under the new experimental conditions, the current study reveals cue-specific allocentric neural representations of spatial locations in the human retrosplenial cortex for the first time. This finding enriches our understanding of how the brain processes diverse sources of spatial information for cognitive map formation.
### Abbreviations

<table>
<thead>
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<th>Region</th>
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<tr>
<td>Retrosplenial cortex</td>
<td>RSC</td>
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<td>Medial temporal lobe</td>
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<td>Hippocampus</td>
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<td>Parahippocampal cortex</td>
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<td>Perirhinal cortex</td>
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<td>Anterior-lateral entorhinal cortex</td>
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<td>Posterior-medial entorhinal cortex</td>
<td>pmEC</td>
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INTRODUCTION

How do we keep track of our location as we move about in an environment? Positional coding can rely both on environmental landmarks and self-motion cues, which provide discrete and continuous information, respectively. While one’s position can be immediately deduced upon seeing a familiar landmark, self-motion cues - involving body-based cues and optic flow - allow for path integration during locomotion. Given the substantial body of evidence that landmark-based navigation and path integration recruit relatively independent cognitive (Chen et al., 2017; Etienne et al., 1996) and neural processes (Chen et al., 2019; Knierim et al., 2014), a crucial inquiry pertains to whether these two modes of navigation invoke common or distinct spatial representations in the brain. Resolving this question would provide significant insights into a fundamental question in spatial navigation – how the human brain integrates different sources of spatial information to construct a coherent cognitive map (O’Keefe & Nadel, 1978; Steel et al., 2021; Tolman, 1948).

In non-human animals, positional codes have long been observed in the form of hippocampal place and entorhinal grid cells. Importantly, while some studies suggest that hippocampal spatial maps are cue-specific (Geva-Sagiv et al., 2016), others showed inconclusive results (Markus et al., 1994; Quirk et al., 1990; Save et al., 2000). Furthermore, this cue specificity appears to depend on the behavioral relevance of the cues (Radvansky et al., 2021). In contrast, a significant body of evidence has indicated cue-specific spatial coding in entorhinal cortex, where different subregions process different types of spatial information. Grid cells in medial entorhinal cortex (MEC) have been frequently implicated in path integration (Gil et al., 2018; Ying et al., 2023). Conversely, the lateral entorhinal cortex (LEC) contains cells that exhibit neuronal activity modulated by the animal’s distance to local objects (Deshmukh & Knierim, 2011; Wang et al., 2018). In partial support of these findings, grid-cell-like activity, which is associated with path integration (Bierbrauer et al., 2020; Stangl et al., 2018), has been observed in the human EC and is predominantly localized to the pmEC (Doeller et al., 2010).

Beyond EC and the hippocampus, position-selective firing is also common in retrosplenial cortex (RSC; Mao et al., 2017; Miller et al., 2021). The rodent RSC integrates different types of idiothetic and allocentric information, including locomotion, head direction, position, and landmark information to support spatial cognition (Stacho & Manahan-Vaughan, 2022). A defining feature of the positional codes in RSC is that they typically evolve at later stages of learning (Miller et al., 2019). Critically, place-cell-like cell populations in RSC largely maintain consistent collective firing patterns regardless of environmental illumination (Mao et al., 2017), which provides preliminary evidence for cue-independent spatial representations.
In humans, the question of cue specificity of spatial coding remains relatively unexplored. One notable exception is an fMRI study by Huffman & Ekstrom (2019) who varied body-based self-motion cues across different environments. Their findings provide preliminary evidence for cue-independent spatial representations in a large-scale brain network, including RSC and the hippocampus.

In addition, our recent fMRI study employed a spatial localization task that allowed for a direct comparison between landmark-based navigation and path integration within the same navigation task and the same environment (Chen et al., 2019). We found that the anterior-lateral (alEC) and posterior-medial EC (pmEC) in the right hemisphere were sensitive to inter-location distance for landmark-based navigation and optic-flow-based path integration, respectively. These findings provide preliminary evidence for cue-specific spatial coding in EC, with different subregions encoding different cues.

However, the generalizability of our previous findings remains uncertain, because multiple factors can influence the neural dynamics of spatial coding, including learning stage (Diersch et al., 2021; Patai et al., 2019; Wolbers & Büchel, 2005) and task difficulty (Patai et al., 2019). Furthermore, this study did not detect neural coding of inter-location distance in other brain regions crucial for navigation such as the hippocampus and RSC. To address these issues, the current study modified the virtual navigation task used in our previous study, in which participants navigated along a linear track based on either path integration cues or visual landmarks. To preview, while participants were clearly able to learn spatial locations based on either cue type, we observed little evidence of spatial coding in the entorhinal cortex. In contrast, there was strong evidence for cue-specific allocentric spatial representations in RSC. Nevertheless, the brain regions involved in successful navigation were different from our previous study, suggesting overall distinct neural mechanisms between the two studies.

MATERIALS and METHODS

Participants

Twenty healthy adult volunteers from the Magdeburg community participated in this experiment (10 male; mean (± SD) age = 25.35 (±3.19) years). All participants were right-handed, had normal or corrected-to-normal vision, and had no neurological diseases. Three additional participants were tested but were excluded from data analysis, either because they dropped out in the middle of the experiment or because the fMRI data were corrupted by technical problems. All participants gave
written informed consent prior to the experiment and received monetary compensation after the experiment. The experiment was approved by the Ethics Committee of the University of Magdeburg.

The experiment took place on three separate days. On the first day (referred to as Pre-scan_day), participants received behavioral training. MRI scanning took place on the second day (MRI_day1) and the third day (MRI_day2), as illustrated in Figure 1c. The decision to scan participants for two separate days was motivated by the goal of acquiring a substantial number of trials to enhance the statistical power of the study. For the majority of participants, the time interval between Pre-scan_day and MRI_day1 ranged from 1 to 6 days (mean interval: 3.75 days); the time interval between MRI_day1 and MRI_day2 ranged from 1 to 7 days (mean interval: 5.35 days). Due to logistical constraints, three participants experienced a longer time interval of 14 or 17 days. However, given that these participants exhibited no discernible differences in terms of their behavior or fMRI results compared to other participants, they were included in the subsequent analyses.

For the following reasons, we determined our current sample size of 20 participants was appropriate to yield sufficient statistical power. First, our sample size was comparable to a recent fMRI study (Huffman & Ekstrom, 2019) that investigated cue-specificity of spatial representations in the human brain. Second, our sample size was closely matched to that of our previous study (Chen et al., 2019), which employed a similar design and analysis methods and involved 22 participants. Importantly, in the current study, we included a considerably larger number of effective trials (i.e., 160 trials per cue type) compared to Chen et al. (2019) (i.e., 40 trials per cue type). Given that statistical power of fMRI experiments depends both on the number of trials and the number of participants (Murphy et al., 2007), the current study possessed a higher empirical statistical power compared to Chen et al. (2019). Finally, we estimated the empirical statistical power (based on 20 participants) for replicating the landmark-related neural coding detected in the right aEC in the ROI-based analysis; the calculated statistical power amounted to 0.77, which closely approximates the commonly accepted threshold of 0.8.

Virtual environment

Two distinct virtual environments were created and rendered in Worldviz 5.0 (https://www.worldviz.com): a city environment and a nature environment (Figure 1a). Both environments shared an identical object layout arranged on a linear track. An arrow set and a tree were positioned at the two ends of the object layout. The arrow set consisted of three identical red arrows positioned at the same position but at different heights from the ground. The tree was
positioned with a 0.5m offset to the left relative to the imaginary midline of the linear track. Between
the arrow set and the tree, four balls of different colors were positioned at four predetermined test
locations. These test locations were evenly spaced along the linear track, with intervals of 4m. The
surface of the linear track was uniformly textured but rendered in different colors for each
environment. Likewise, the arrow set and the tree remained consistent in their appearance but
exhibited different colors in the two environments. To further differentiate the two environments, the
order of the four balls was reversed while their respective test locations remained constant in the two
environments. Additionally, the background view and the ground texture beyond the linear track
differed between the two environments.

Experimental design

The primary experimental task was the “location identification task”, designed to dissociate landmarks
and self-motion cues in each trial. To familiarize participants with the positions of the four test
locations, they also completed a learning task at times. Details regarding the learning task can be
found in Extended Data 1 (Section 1.1; and see all supplementary methods and results in Extended
Data 1).

In the ‘location identification task’, participants were passively transported to one of the four
test locations, and were required to recall the color of the ball positioned at that location. The ball
remained invisible throughout the trial. The temporal sequence of a trial is depicted in Figure 1b (also
refer to the video, specifically the segment titled “TEST: location identification task”). In each trial, the
initial position of the passive movement was randomly selected from a uniform distribution ranging
from -18 m to -4 m (Figure 1a; the arrow set was positioned at 0 m). Once the passive movement
ceased, participants’ first-person perspective was fixed at the test location for 4 seconds, after which
they had to report the color of the ball they believed was positioned at their current location.
Importantly, the order of the four answer options displayed on the screen was randomized on a trial-
by-trial basis, and participants pressed a designated button on the joystick to cycle through the
options. This setup ensured that each test location was not associated with a fixed position on the
screen or a consistent pattern of joystick movements. To prevent the use of timing or counting
strategies, the movement speed during the passive transport was randomly sampled from a uniform
distribution ranging from 2 m/s to 5 m/s on a trial-by-trial basis. Accuracy was emphasized, but
participants were instructed to not spend longer time than necessary.
To dissociate the use of self-motion cues and landmark cues, an approach similar to our previous study was employed with several adjustments (Chen et al., 2019). This manipulation followed the logic of dissociating landmark and self-motion cues in well-established behavioral paradigms (Bates & Wolbers, 2014; Chen et al., 2017; Nardinì et al., 2008). In the self-motion condition, both the arrow set and the linear track texture were visible. As the arrow set served as a reference point for path integration based on traveled distance, participants were able to perform path integration using optic flow after passing the arrow set. However, the landmark was not visible, thereby eliminating landmark-based navigation. To prevent participants from associating the test locations with spatially isolated features on the ground, which would resemble a landmark-based navigation strategy (e.g., the red ball’s position was within the brightest patch of the ground), both the texture of the linear track and the floor texture outside the linear track were randomly shifted along the linear track on a trial-by-trial basis, following a uniform distribution ranging from -50 m to 50 m.

In contrast, in the landmark condition, the landmark was visible, and it was the only cue participants could use for localization. To eliminate path integration, the arrow set was removed, and the ground texture of the linear track was left blank to remove texture-based optic flow cues. While there was still peripheral optical flow originating from the floor texture outside of the linear track, participants could not employ path integration effectively. This was due to randomized starting position of the passive movement on a trial-by-trial basis and the absence of the reference point for path integration (i.e., the arrow set). Consequently, participants lacked the necessary information to accurately gauge the traveled distance required to reach a specific ball position. The cue manipulation in the landmark condition aligns with the disorientation manipulation commonly used in spatial navigation studies to eliminate self-motion information (Cheng, 1986; Sutton et al., 2010).

Experimental procedure

The experiment took place on three separate days: the first day (Pre-scan_day) consisted of behavioral training, while the 2nd day (MRI_day1) and 3rd day (MRI_day2) involved MRI scanning (Figure 1c). The purpose of the behavioral training was twofold: to familiarize participants with the task and to ensure the formation of stable memories of the four test locations before the MRI scanning sessions. For further details regarding the behavioral training on the Pre-scan day, please refer to Extended Data 1 (Section 1.2).

Both MRI scanning sessions followed the same procedure. At the beginning of each scanning day, participants were re-familiarized with the task through a practice session while undergoing
structural MRI scanning inside the scanner. This practice stage lasted approximately five minutes and was not analyzed further. Following the practice stage, participants performed the ‘location identification task’ during the subsequent functional scanning (Figure 1b; also refer to the video – “TEST: location identification task”).

Each fMRI session consisted of a total of eight runs, with two runs for each of the four combinations of cue condition (self-motion vs. landmark) and environment (city vs. nature). The eight runs were organized into two blocks, where each block comprised four runs corresponding to the four condition combinations. Within each block, the four condition combinations were semi-randomized using Latin square designs and with the restriction that the combinations occurring in two successive runs were different in each fMRI session.

A continuous carry-over design (Aguirre, 2007) was employed to present the trials. We selected eight de Bruijn sequences with high detection power and low correlation coefficient. These de Bruijn sequences were generated using a 2nd order counterbalancing approach known as the ‘path-guided’ method (Aguirre et al., 2011). Each de Bruijn sequence consisted of five event types: fixation periods at the four test locations, where participants stayed at the test locations for 4 seconds, and null events, during which participants fixated their gaze on a centrally displayed cross against a blank screen. Each de Bruijn sequence consisted of 25 events in total, with five repetitions for each event type. To allow the hemodynamic response to reach a steady state before the start of the sequence, the final event in the sequence was duplicated and placed at the beginning. Although this duplicated event was modeled in the first-level GLMs, it was not utilized for the main fMRI analyses. Consequently, each run consisted of 20 effective trials for the main fMRI analyses, with five trials corresponding to each of the four test locations. These eight de Bruijn sequences were randomly assigned to the eight runs in each scanning session for each participant.

During each MRI session, the functional scanning lasted approximately 1 hour, with the total scanning time lasted up to approximately 1.75 hours.

Comparisons with the task in Chen et al. (2019)

While the current task shared similarities with the task used in our previous study (Chen et al., 2019) in terms of utilizing a linear track navigation task and dissociating landmarks and self-motion cues, it is important to highlight some key differences. First, participants in our previous study completed the entire experiment within a single day, learning the spatial location of a single target over a brief period (~15 minutes) before undergoing functional scanning. In contrast, in the current study, participants
received extensive training (~45 minutes) on a separate day prior to the two MRI scanning sessions. Their behavioral performance had reached a plateau prior to the scanning and remained stable throughout the scanning period (Extended Data 1, Figure E2), indicating a relatively late spatial memory stage compared to Chen et al. (2019).

Second, we made the four test locations much easier to discriminate by increasing the spatial distances among them, i.e., distance between two adjacent test locations was four virtual meters compared to two virtual meters in the previous study. This modification also resulted in longer temporal intervals between successive location occupation events, as participants needed to traverse longer distances to reach the test locations.

Third, the starting position was randomized on a trial-by-trial basis for both cue conditions in the current study. This allowed for evaluating allocentric positional codes while excluding potential influences of path length for each cue type. In contrast, our previous study implemented this dissociation only in the landmark condition, as the starting position remained fixed for the self-motion condition.

Fourth, unlike our previous study where participants memorized the position of a single target location and judged the relative positions of four equidistant test locations to the target location positioned at the center of the test location layout, the current task required participants to explicitly memorize and recognize the positions of the four equidistant test locations.

Fifth, in our previous study, flashing dots positioned on the floor were used to deliver optic flow information, which are not representative of the optic flow inputs in our daily life. The current study used textured carpets to provide a more realistic optic flow experience.

Sixth, while our previous study employed a single virtual environment, we incorporated two distinct background environments. This adjustment aimed to explore potential effects of the environment on spatial coding, which has been frequently investigated in previous studies (Colgin et al., 2008). Environment served as a secondary factor in our design, while cue type remained the primary focus.

Lastly, while our previous study incorporated both a high-reliability condition and a low-reliability condition for each cue type, in the current study, we did not manipulate cue reliability and the spatial cues were relatively high in reliability. First, our current focus has shifted away from examining the influence of cue reliability on spatial representations. In addition, our previous study has shown that spatial representations were discernible only when cues reached a sufficient level of reliability. Finally, by excluding the low-reliability conditions, we could maximize the number of trials,
thereby enhancing statistical power for detecting and characterizing the neural codes of positional information.

**MRI acquisition**

The protocol for MRI acquisition was the same as our previous study (Chen et al., 2019). Structural and functional images were acquired in a 7T MR scanner (Siemens, Erlangen, Germany) at the Leibniz Institute for Neurobiology in Magdeburg with a 32-channel head coil (Nova Medical, Wilmington, MA).

A high-resolution whole-brain T1-weighted structural scan was acquired with the following MP-RAGE sequence: \( \text{TR} = 1700 \text{ ms}; \text{TE} = 2.01 \text{ ms}; \text{flip angle} = 5^\circ; \text{slices} = 176; \text{orientation} = \text{sagittal}; \text{resolution} = 1 \text{ mm isotropic.} \)

A partial-volume turbo spin echo high-resolution T2-weighted structural scan was acquired perpendicular to the long axis of the hippocampus (\( \text{TR} = 8000 \text{ ms}; \text{TE} = 76 \text{ ms}; \text{flip angle} = 60^\circ; \text{slices} = 55; \text{slice thickness} = 1 \text{ mm}; \text{distance factor} = 10\%; \text{in-plane resolution} = 0.4 \times 0.4 \text{ mm}; \text{echo spacing} = 15.1 \text{ ms}, \text{turbo factor} = 9, \text{echo trains per slice} = 57). Functional scans were acquired with a T2*-weighted 2D echo planar image slab centered on the hippocampus and parallel to its long axis (\( \text{TR} = 2000 \text{ ms}, \text{TE} = 22 \text{ ms}; \text{flip angle} = 85^\circ; \text{slices} = 35; \text{resolution} = 1 \text{ mm isotropic, parallel imaging with grappa factor} \text{ 1, echo spacing} = 0.82 \text{ ms}). We also obtained 10 volumes of whole brain functional scans for the purpose of co-registering anatomical masks obtained on the T2-weighted structural scan to functional scans with a MPRAGE sequence (\( \text{TR} = 5000 \text{ ms}, \text{TE} = 22 \text{ ms}; \text{flip angle} = 85^\circ; \text{slices} = 100; \text{resolution} = 1.6 \text{ mm isotropic}). The T1-weighted structural image was bias-corrected in SPM12. The functional scans were motion and distortion corrected online via point spread function mapping (In & Speck, 2012). Figure 2a shows the T2-weighted structural scan and a functional scan overlaid on the T1-weighted structural scan for an exemplary participant.

**Anatomical masks for regions of interest (ROIs)**

As our regions of interest (ROI), we focused on the entorhinal subregions, hippocampus, retrosplenial cortex (RSC), parahippocampal cortex (PHC), and perirhinal cortex (PRC). To illustrate, Figure 2b-d displays the anatomical masks for an exemplary participant.

As shown in Figure 2c, brain regions in the medial temporal lobe (MTL) were manually segmented on each participant’s T2-weighted structural scan in ITK-SNAP (Yushkevich et al., 2006; http://www.itksnap.org/pmwiki/pmwiki.php), following an established protocol (Berron et al., 2017). EC was further divided into the anterior-lateral subregion (aEC) and the posterior-medial subregion (pMEC), following the procedure developed in Chen et al. (2019). As shown in Figure 2d, the
hippocampus was further segmented into different subfields (CA1, CA2, CA3, subiculum (SUB),
dentate gyrus (DG), and tail).

RSC mask was automatically extracted from each participant’s T1-weighted structural scan
(bias-corrected in Advanced Normalization Tools (ANTs)) in Freesurfer (Dale et al., 1999), using the
‘recon-all’ command. RSC was defined as the posterior-ventral portion of the cingulate gyrus, which
mainly consists of BA29/30. Note that the definition of RSC is anatomically different from the
retrosplenial complex, which is a functionally defined region typically extending into the parieto-
occipital sulcus (Epstein, 2008). In addition, although different functional subregions have been
identified within the rodent and monkey RSC (Vann et al., 2009), there are currently no established
standards for demarcating functional subregions within RSC in the human brain.

The anatomical mask for RSC, along with the T1-weighted structural scan, was first co-
registered to the mean whole-brain functional scan, which had already been co-registered to the
mean functional scan; then the co-registered anatomical mask was resliced using nearest-neighbor
interpolation, with the mean functional scan as the reference image. The anatomical masks for the
MTL regions were co-registered to the mean functional scan of the first scanning day in SPM12, using
the following procedure: first, the mean whole-brain functional scan was co-registered to the mean
functional scan; second, the T2-weighted structural scan, along with the anatomical masks, were co-
registered to the mean whole-brain functional scan obtained from the first step; third, the co-
registered anatomical masks were re-sliced using nearest-neighbor interpolation, with the mean
functional scan as the reference image.

Behavioral and fMRI statistical analyses

Behavioral data analysis

We calculated behavioral accuracy based on whether the answer was correct (coded as 1) or not
(coded as 0), with a chance level of 0.25. For the two scanning days, the first trial of the sequence in
each block was not included in the analysis, because it was not included in the main fMRI analyses and
did not appear to differ from other trials in the sequence.

fMRI univariate adaptation analyses

To investigate spatial coding in the brain, we conducted the location-based fMRI adaptation analysis,
based on the logic that the closer the preceding location is to the currently occupied location, the
lower the brain activation. To ensure effective comparisons between the current study and our previous study, the fMRI univariate adaptation analyses were conducted in the same way as in our previous study (Chen et al., 2019). In particular, the first-level GLMs were constructed in the same manner as in our previous study.

First-level analysis. To assess fMRI adaptation in relation to inter-location distance, we constructed a first-level general linear model (GLM1). Along with the regressors that modeled the location occupation periods (Figure 1b, phase 4 ‘location occupation’), we included parametric regressors modeling the modulatory effects of spatial distance between sequentially visited locations. These parametric regressors captured the continuous variation of inter-location distance, specifically with values of 0m, 4m, 8m, and 12m. Separate regressors were created to model the location occupation periods that were not suitable for adaptation, i.e., being preceded by a null event or being in the first trial. To control for potential effects of the passive movement stage on the adaptation effects associated with the ensuing location occupation period, we included regressors modeling the passive movement phase for each run and each cue type, irrespective of the test location. Events were modeled with boxcar regressors convolved with the canonical hemodynamic response function (plus temporal derivative), as implemented in SPM12. Head motion parameters (three rotation parameters and three translation parameters) were included as nuisance regressors, separately for the 16 runs.

To visualize the adaptation effects, we constructed a separate first-level GLM (GLM2), in which separate regressors modeled the location occupation periods with different inter-location distances (i.e., 0m, 4m, 8m, and 12m). The beta estimates of these regressors were then plotted as a function of inter-location distance.

It is important to note that we did not include separate regressors for all phases in the location identification task. Since natural navigation involves consecutive phases without blank intervals, using separate regressors for each could lead to severe multicollinearity issues, compromising reliability of the parameter estimates. This concern is heightened by our inclusion of the time derivatives for each event regressor, which doubled the number of regressors in the GLM. Therefore, we deliberately minimized the number of regressors, focusing on phases critical for hypothesis testing and with substantial duration to influence neural responses noticeably. This selective approach aimed to balance between capturing essential aspects of the experimental design and maintaining statistical integrity. Detailed rationale follows.
First, phase 4 “location occupation” was of primary interest, hence we considered it essential to model this phase explicitly in the GLM. Modeling this phase allowed us to investigate the neural responses associated with specific spatial locations, akin to the investigation of place-sensitive cells, which fire when the mobile agent occupies certain locations in space.

Second, phase 2 “movement” occupied a substantial portion of the trial and contained sensory information that markedly differed between cue conditions. Consequently, modeling this phase was crucial for accounting for its potential impact on neural responses associated with the location occupation phase.

Third, phase 1 “start” and phase 3 “location arrival” were not modeled in the GLM due to their brief durations. The “start” phase averaged 0.7 s in both studies, and the “location arrival” phase on average lasted approximately 0.5 s in our previous study and 2 s in the current study. Furthermore, the “location arrival” phase immediately preceded the location occupation phase with no breaks, making it challenging to separate these phases effectively.

Fourth, since phase 5 “response” and phase 6 “feedback” followed immediately our phase of interest (phase 4 “location occupation”), modeling these two phases would introduce multicollinearity issues. In addition, these two phases were the same regardless of cue condition and occupied location, and in the current study we designed the response mode in such way that any location choice was not associated with any consistent pattern of finger movements. Therefore, these two phases should not confound the results associated with the “location occupation” phase.

Nevertheless, to thoroughly evaluate the impact of the preceding navigation experiences on location-based adaptation associated with the location occupation phase, we constructed another GLM, in which the regressors modeling the “movement” phase were extended to include the entire navigation stage (phase 1 + phase 2 + phase 3). Modeling these phases together as a single navigation event considered their continuous nature, avoiding multicollinearity issues. Notably, the main findings on location-based adaptation remained consistent, as the parametric modulation regressors modeling location-based adaptation were minimally correlated with the regressors modeling the extended movement phase in this revised GLM1 (|rs| < 0.011), similar to the original GLM1 (see details in the ‘Control Analyses – Passive Movement’ section). This consistency underscores the robustness of our findings across analyses.

Second-level ROI-based analysis. First, beta estimates for adaptation of all voxels in each ROI were averaged for each participant. Next, participant-specific beta estimates of adaptation were tested
using directional one-sample t tests, yielding the uncorrected significance levels. We performed one-sided statistical tests because we hypothesized that BOLD responses should decrease as the distance between successively visited locations decreased, i.e., positive adaptation. In addition, negative adaptation is difficult to interpret (Barron et al., 2016). To correct for multiple comparisons, we employed the nonparametric permutation-based maximum-t-statistic approach (Extended Data 1, Section 1.3).

For each group-level t test, we calculated the Bayes factor (BF\(_{10}\)), which indicates the relative likelihood of the alternative hypothesis (i.e., the group mean was greater than 0) over the null hypothesis (i.e., the group mean was not greater than 0) (Rouder et al., 2009). The effect size scale (r) adopted was 0.707. A BF\(_{10}\) greater than 3/10/30 indicates moderate/strong/very-strong evidence for the alternative hypothesis, whereas a BF\(_{10}\) less than 0.333/0.1/0.03 indicates moderate/strong/very-strong evidence for the null hypothesis (Jeffreys, 1961). BF\(_{10}\) was also calculated in other ROI-based group-level fMRI analyses.

Statistical outliers were identified using the boxplot rule, i.e., a value would be considered as an outlier if it is larger than 3rd quartile + 3* interquartile range or smaller than 1st quartile – 3 * interquartile range. Statistical outliers were winsorized to the nearest inlier (Reifman & Keyton, 2010).

**Second-level voxel-wise analysis.** Voxel-wise analysis is an important supplement to the ROI analysis. Participant-specific adaptation maps were normalized to the Montreal Neurological Institute (MNI) template and spatially smoothed with 3mm isotropic FWHM. We conducted directional one-sample t-tests against 0. To localize adaptation effects within our ROIs, we created group-level anatomical masks for small-volume-correction (Extended Data 1, Section 1.4). Multiple comparisons were corrected using the nonparametric permutation-based approach (Nichols & Holmes, 2002), using the voxel-level inference approach or the cluster-level inference approach (voxel-wise T > 3). To explore beyond our ROIs, we corrected for multiple comparisons across the entire volume, also using the nonparametric permutation-based test.

**fMRI adaptation pattern similarity analysis**

The primary goal of this study was to investigate whether or not the neural representations of the four test locations were specific to or independent of the underlying cue type (self-motion vs. landmark). Since the voxel-wise adaptation effects served as an index of spatial coding, we investigated cue-specificity of this coding with an adaptation pattern similarity analysis. This analysis
is analogous to multivariate representational similarity analysis (RSA), but with voxel-wise adaptation magnitude instead of voxel-wise activation level as the basic element. If the voxel-to-voxel adaptation pattern differed between landmarks and self-motion cues, this would suggest dissociable neural representations evoked by the two cue types.

The adaptation pattern similarity analysis consisted of several steps. First, an adaptation vector was estimated for each of the 16 runs for each cue type, containing adaptation estimates (signed) of all voxels in a given ROI. This resulted in a total of eight adaptation vectors per cue type. The secondary factor ‘environment’ was averaged out by calculating the mean of two adaptation vectors from adjacent runs from different environments for the same cue type on a voxel-by-voxel basis (see a similar treatment of averaging out factor-of-not-primary-interest in Shine et al., 2019).

Next, the adaptation pattern similarity was computed in a cross-validated manner by calculating the Pearson correlation between pairwise adaptation vectors (Walther et al., 2016). Specifically, within-cue similarity was calculated as the Pearson correlation between adaptation vectors of the same cue type. In contrast, between-cue similarity was computed by correlating adaptation vectors from different cue types. The final estimates of within-cue similarity and between-cue similarity were obtained by averaging all the Pearson correlations (Fisher-transformed) calculated from all possible pairs of adaptation vectors.

Finally, we calculated an adaptation pattern distinction score by subtracting the between-cue similarity from the within-cue similarity. The adaptation pattern distinction score was then tested against zero with a one-sided t test, as we expected the adaptation pattern to be more similar within the same cue type than between different cue types. A positive adaptation pattern distinction score indicates that the spatially distributed adaptation pattern differed between different cue types.

To verify that our findings were not solely driven by a particular environment, we also conducted the analysis for each environment separately.

fMRI analysis of successful navigation

To assess the involvement of brain regions in the navigation task, we constructed GLM3 to compare brain activation during the “location occupation” phase between correct trials and incorrect trials. This approach is commonly employed to infer brain regions’ engagement in cognitive tasks (Chrastil et al., 2015; Pessoa et al., 2002). To ensure consistency and effective comparisons, this analysis was conducted in exactly the same manner as in our previous study (Chen et al., 2019). In particular, the first-level GLMs were constructed in the same way as in our previous study.
First-level analysis. We constructed GLM3, which had a structure similar to GLM1, with three differences. First, there were no parametric regressors that modeled the modulatory effects of inter-location spatial relation on BOLD signals. Second, there were separate event regressors modeling the “location occupation phase” for the incorrect trials and the correct trials separately, collapsed across the four test locations, resulting in 2 (landmark vs. self-motion) * 2 (correct vs. incorrect) = 4 event regressors. Third, the scans were concatenated across all the 16 runs, because some subjects did not make a single mistake in some runs, meaning that no trials could be labeled as “incorrect” in the run. In the scan concatenation, 16 effect regressors were included to model the average activity in each run, and each run had its own set of head motion regressors.

Second-level ROI-based analysis. For each ROI, mean beta estimates of brain activation during the “location occupation” phase were submitted to a repeated measures ANOVA with cue type (landmark vs. self-motion) and correctness (correct vs. incorrect) as independent variables. Statistical outliers were identified using the boxplot rule, i.e., a value would be considered as an outlier if it is larger than 3rd quartile + 3* interquartile range or smaller than 1st quartile – 3 * interquartile range. Statistical outliers were then winsorized to the nearest inlier (Reifman & Keyton, 2010).

Second-level voxel-wise analysis. The participant-specific beta images were normalized to the MNI template. The normalized beta images were then spatially smoothed with a 3 mm full-width half-maximum (FWHM) gaussian filter. To obtain participant-specific contrast images for evaluating the main effect of successful navigation in the within-subjects design in GLM3, we applied appropriate weighting schemes to the participant-specific normalized beta images, assigning weights [1, -1, 1, -1] to the beta images of the landmark correct, landmark incorrect, self-motion correct, and self-motion incorrect conditions. Next, similar to the univariate adaptation analysis, a nonparametric 2-tailed one-sample t test was conducted on the contrast images for the main effect of successful navigation, using the SnPM13 toolbox (Nichols & Holmes, 2002). We created group-level anatomical masks for small-volume-correction (Extended Data 1, Section 1.4). To explore beyond our ROIs, we corrected for multiple comparisons across the entire volume.

RESULTS
Behavioral results

Behavioral evidence for a dissociation of landmarks and self-motion cues

We focused on behavioral data obtained during the two scanning sessions (Figure 3). We submitted behavioral accuracy to a repeated-measures ANOVA with cue type, test location, scanning session, and environment as independent variables. This analysis revealed main effects of cue type (F(1,19) = 10.552, p = 0.004, η_p^2 = 0.357) \(a_1\) and location (F(3,57) = 9.170, p < 0.001, η_p^2 = 0.326) \(a_2\), which were qualified by a significant interaction between the two variables (F(3,57) = 25.051, p < 0.001, η_p^2 = 0.569) \(a_3\): in the landmark condition, behavioral accuracy increased as the test location got closer to the tree (i.e., the anchoring point for landmark-based navigation), whereas in the self-motion condition, behavioral accuracy increased as the test location got closer to the arrows (i.e., the anchoring point for path integration). Accordingly, the interaction between cue type and the linear trend of test location was significant (t(57) = 8.487, p < 0.001) \(a_4\). Further analyses revealed that the linear trend of test location was significant in both the landmark condition (t(112) = 3.020, p = 0.003) \(a_5\) and the self-motion condition (t(112) = 9.798, p < 0.001) \(a_6\). No effects involving environment or scanning session were significant (ps > 0.3, η_p^2 < 0.062), meaning that behavioral performance was similar in the two environments and stable across the two scanning sessions.

Furthermore, we employed a cognitive modeling approach to investigate whether using different navigational cues specifically affected representational precision by disentangling representational precision, response bias, and potential attentional lapse. We found that representational precision exhibited a similar pattern as the behavioral accuracy as a function of cue type and test location, after accounting for response bias and attentional lapse (Extended Data 1, Section 2.1, Figure E1).

Finally, further analysis that also included data from the Pre-scan day showed that (i) performance had already reached ceiling towards the end of the Pre-scan day, and (ii) performance remained stable across the two MRI scanning days (Extended Data 1, Section 2.2, Figure E2).

In summary, the key behavioral finding was the distinct profiles of behavioral accuracy observed across test locations in the two cue conditions. Importantly, this finding was not confounded by response bias or attentional failure, indicating the success of our cue dissociation manipulation. Finally, participants’ behavioral performance had reached a plateau prior to the MRI scanning.

fMRI results
FMRI analyses focused on the location occupation phase of the location identification task, when the camera was panned down to the ground to render visual inputs identical between the landmark condition and the self-motion condition (Figure 1b, phase 4). We investigated whether BOLD signals contained information pertaining to the spatial relations among the test locations. To this end, we employed fMRI adaptation, a well-documented phenomenon in which BOLD signal exhibits a reduction when the current location is preceded by the same or a nearby location, with the degree of suppression proportional to the spatial proximity of the two locations (Barron et al., 2016; Chen et al., 2019; Morgan et al., 2011).

To evaluate a potential impact of scanning session and environment on adaptation, we conducted an omnibus repeated-measures ANOVA on adaptation, with ROI (RSC, hippocampus, PRC, PHC, left aEC, left pmEC, right aEC, right pmEC), cue type, environment, and scanning session as independent variables. While the main effect of ROI was significant ($F(7,133) = 5.180, p < 0.001, \eta^2_p = 0.214$), there were no significant effects involving environment or scanning session ($Fs < 3.1, ps > 0.09, \eta_s^2 < 0.15$), which mirrors the behavioral results. Therefore, we averaged adaptation effects across both environments and scanning sessions for all the further analyses.

Entorhinal cortex shows little evidence for positional coding for landmarks

First, we examined whether we could replicate our previous observation of adaptation-based positional coding in the entorhinal subregions (Chen et al., 2019). The ROI-based analysis revealed no significant adaptation in any of the entorhinal subregions in either hemisphere, even at the uncorrected significance level ($ts < 1.52, ps_{1-tailed} > 0.07, BF_{10} < 1.14$; Figure 4a; see Table 1 for detailed statistics). Consistently, the voxel-wise analysis revealed no significant adaptation for either cue type in the left EC when using the group-level anatomical mask of the left EC for small-volume-correction ($Ts < 4.5, ps_{FWE-corr} > 0.1$), and no significant adaptation for either cue type in the right EC when using the group-level anatomical mask of the right EC for small-volume-correction ($Ts < 3, ps_{FWE-corr} > 0.8$).

RSC shows strong evidence for positional coding for both landmarks and self-motion cues

Next, we examined whether adaptation existed in other ROIs, i.e., RSC, hippocampus, PHC, and PRC. Results are depicted in Figure 4b, and detailed statistics can be found in Table 1.
RSC showed significant adaptation in both the landmark condition and the self-motion condition (landmark, $t(19) = 2.127$, $p_{1\text{-tailed}} = 0.023$, $BF_{10} = 2.843$; self-motion, $t(19) = 2.940$, $p_{1\text{-tailed}} = 0.004$, $BF_{10} = 11.769 > 10$). As shown in Figure 4d (left), RSC’s activation increased linearly with increasing inter-location distance in the self-motion condition. However, the landmark condition exhibited a different pattern: brain activation was higher for all non-zero inter-location distances relative to the zero inter-location distance (i.e., when two successively visited locations were the same), but remained stable for different non-zero distances. This implies that in the landmark condition, RSC adaptation was related to location identity rather than inter-location distance.

Therefore, we modelled location identity by setting the value of the parametric regressor to 0 if the preceding test location was the same as the current one and to 1 if the preceding test location was different from the current one; we observed strong evidence for location-identity-based adaptation for landmarks ($t(19) = 3.356$, $p_{1\text{-tailed}} = 0.002$, $BF_{10} = 25.919 > 10$), as shown in Figure 5b (dark blue bar). Furthermore, when we disentangled location identity and inter-location distance in the same first-level GLM by including both variables as the parametric modulation regressors (Mumford et al., 2015), the unique contribution of location identity to adaptation - after accounting for inter-location distance - was significant ($t(19) = 1.963$, $p_{1\text{-tailed}} = 0.032$, $BF_{10} = 2.191$; one outlier winsorized: $t(19) = 2.008$, $p_{1\text{tailed}} = 0.030$, $BF_{10} = 2.353$; light blue bar). In contrast, the unique contribution of inter-location distance – after accounting for location identity – was not significant ($t(19) = 0.093$, $p_{1\text{tailed}} = 0.464$, $BF_{10} = 0.249$). These results indicate that adaptation was predominantly driven by location identity rather than inter-location distance for landmarks in RSC.

Besides RSC, PHC showed significant adaptation in the self-motion condition ($t(19) = 2.759$, $p_{1\text{-tailed}} = 0.006$, $BF_{10} = 8.492$), as shown in Figure 4b. In this condition, PHC activation increased linearly as inter-location distance increased, although there was a slight drop at the longest inter-location distance (=12m; Figure 4d, right). However, unlike RSC, the unique contribution of either location identity or inter-location distance was not significant ($ts < 0.9$, $ps > 0.2$, $BF_{10} < 0.51$), meaning these two forms of adaptation could not be disentangled.

Other ROIs (PRC, hippocampus, and hippocampal subfields) did not show significant adaptation, even at the uncorrected significance level ($ts < 1.5$, $ps > 0.08$, $BF_{10} < 1$) (Figure 4b&c)).

To ascertain the robustness of the adaptation effects observed in RSC and PHC, we employed a nonparametric maximum-t-statistic multiple comparison correction across all four ROIs and both cue types, resulting in a total of eight one-sample $t$ tests in total (Extended Data 1, Section 1.3). All the aforementioned significant adaptation effects survived the multiple comparison correction: landmark
condition (p_{corrected} = 0.005) and self-motion condition (p_{corrected} = 0.022) in RSC, and self-motion condition in PHC (p_{corrected} = 0.033) exhibited robust statistical significance.

Finally, to further investigate the robustness of the adaptation effects observed in RSC and PHC in the ROI-based analysis, we conducted voxel-wise analysis, using a group-level mask that encompassed all of our ROIs (i.e., bilateral medial temporal lobe plus RSC) for small-volume-correction. In the landmark condition, we observed a significant cluster showing location-identity-based adaptation (k = 1029, p_{FWE-corr} < 0.001; Figure 6), and the peak voxel was within the group-level anatomical mask of RSC (T = 6.76, MNI: 3, -56, 12). Notably, this peak voxel within the RSC mask also represents the second highest level of statistical significance across the entire search volume, and was included in a larger cluster that survived the multiple comparison correction across the entire search volume (K = 4085, p_{FWE-corr} = 0.002). This analysis also revealed two other clusters showing significant location-identity-based adaptation in the parahippocampal, lingual, and fusiform gyri. Conversely, the analysis of inter-location-distance-based adaptation did not yield any significant results (ks < 53, p_{FWE-corr} > 0.25), which mirrors the ROI-based analysis. In the self-motion condition, we observed one significant cluster associated with inter-location-distance-based adaptation (k = 153, p_{FWE-corr} = 0.015). The peak voxel was within the group-level anatomical mask of RSC (Figure 6). Conversely, no significant clusters were found for location-identity-based adaptation (ks < 90, p_{FWE-corr} > 0.06). In brief, the voxel-wise analysis confirmed the ROI-based analysis that revealed significant location-identity-based adaptation for landmarks and inter-location-distance-based adaptation for self-motion cues in RSC. Detailed results of the voxel-wise analysis are summarized in Extended Data 1 (Section 2.3, Figure E4, Table E1).

We also compared the two hemispheres for RSC and HPC in adaptation, and obtained very similar results in the two hemispheres (Extended Data 1, Figure E5).

Successful reconstruction of physical space from adaptation in RSC for self-motion cues

To further characterize the above-mentioned significant adaptation effects observed in RSC and PHC, we asked whether it was possible to reconstruct individual test locations from adaptation effects in these areas. If fine-grained distance information between different locations was contained in the adaptation effect, we should be able to recover the physical space from it. This analysis can also further illustrate the aforementioned distinction between location-identity-based adaptation and inter-location-distance-based adaptation, because only the latter form should contain fine-grained distance information to allow for a successful reconstruction of the physical space.
To address this question, we employed a neural space reconstruction analysis (Figure 5c) that was based on neural distances between different test locations. Neural distance was quantified as a brain region’s activation for one location when preceded by another. Lower activation levels correspond to stronger repetition suppression and closer positioning of two test locations in the neural space (Extended Data 1, Section 1.5).

Regarding RSC, in the landmark condition, the neural representation of space did not correspond to the physical space ($p_{1\text{-tailed}} = 0.741$), with some locations even swapped in order. This observation aligns with the earlier finding that in the landmark condition, the repetition suppression effect only distinguished between identical and different locations, without discerning between different non-zero inter-location distances (Figure 5c). In contrast, in the self-motion condition, the neural representation of space demonstrated a significant resemblance to the physical space ($p_{1\text{-tailed}} = 0.018$). This finding is consistent with the earlier observation that in the self-motion condition, the repetition suppression effect contained fine-grained distance information between different locations (Figure 5c).

Although the preceding results showed that PHC exhibited significant inter-location-distance-based adaptation for self-motion cues, the corresponding reconstructed neural space did not significantly resemble the physical space ($p_{1\text{-tailed}} = 0.252$).

In brief, we could reconstruct the original physical space from adaptation in RSC with respect to self-motion cues, but not based on landmarks. This underscores again that adaptation in this region reflected inter-location distance for self-motion cues but not for landmarks. The inability to reconstruct the physical space through adaptation in PHC for self-motion cues highlights the pivotal role of RSC in representing fine-grained distance information extracted from self-motion cues.

Positional coding in RSC is distinct between cue types

To iterate, the primary goal of this study was to assess the specificity or independence of spatial representations in the brain with respect to landmarks and self-motion cues. The preceding analyses revealed spatial coding for both landmarks and self-motion cues in RSC. As depicted in Figure 6, the retrosplenial clusters exhibiting significant adaptation for landmarks and self-motion cues displayed little overlap. However, it remains to be determined whether the spatial coding in RSC was cue-specific or cue-independent. To answer this question, we conducted two main types of analyses: univariate analysis in either the standard brain or participants’ native brains, and multivariate analysis leveraging spatially fine-grained signals across all voxels within RSC.
Univariate analysis in standard brain. First, we tested differences between cue types in location-based adaptation within RSC. We normalized participant-specific beta images to the MNI template, which were then spatially smoothed. We then conducted a nonparametric permutation-based paired t test, using the group-level anatomical mask of RSC for small volume correction. There were no voxels (p_{FWE-corr} > 0.2, 1-tailed) or clusters (p_{FWE-corr} > 0.45, 1-tailed; cluster-defining threshold: T > 3) showing significant differences between cue types, meaning no positive evidence for cue-specific spatial representations in RSC.

Next, we tested commonalities between cue types in location-based adaptation within RSC, by conducting the conjunction analysis as implemented in the flexible factorial design in SPM12 (Friston et al., 1999). The group-level anatomical mask of RSC was used for small volume correction. There were no voxels (p_{FWE-corr} > 0.35, 1-tailed) or clusters (p_{FWE-corr} > 0.14, 1-tailed; cluster-defining threshold: T > 3) showing significantly location-based adaptation for both cue types, meaning no positive evidence for cue-independent spatial representations in RSC.

In brief, the univariate analyses in the standard brain revealed no positive evidence for either cue-specific or cue-independent spatial representation in RSC.

Univariate analysis in native brain. The preceding univariate analyses were voxel-based and performed in a standard template (i.e., MNI template), which overlooks individual brain variability and may introduce spatial smoothing artifacts. To address these limitations, we conducted another univariate analysis in participants’ native brains. Specifically, we segmented RSC in a biologically valid way in each participant’s brain; if different cue conditions exhibit differential patterns of adaptation change across the RSC portions, it would indicate that different parts of RSC contained spatial coding for different cue types.

Currently, there are no established standards for segregating the human RSC (Vann et al., 2009). To achieve biologically meaningful segmentation, we employed the ConGrads toolbox (Haak et al., 2018), which is a data-driven approach that partitions a brain region into functionally discrete subregions based on voxel-to-voxel functional connectivity patterns (Grady, 2020; Schröder et al., 2015).

First, we applied the ConGrads toolbox to the participant-specific residual scans acquired from GLM1 as a proxy for resting-state functional data (Extended Data 1, Section 1.6). In RSC, we observed a gradient along its long axis, as dictated by the dominant connectopy (Figure 7a), which is in broad
concordance with previous research (Chrastil, 2018; Peer et al., 2019). Notably, we obtained a consistent pattern of results when applying the ConGrads toolbox to a separate functional resting-state dataset acquired at a 3T MRI scanner (Extended Data 1, Section 1.6 & 2.5; Figure E6).

Next, we divided RSC into ten equally-sized portions for each participant based on the dominant mode of the functional connectivity change (Figure 7b). We then submitted location-based adaptation into a repeated measures ANOVA test, with cue type, portion, and environment as independent variables. As shown in Figure 7c-e, the main effect of portion was statistically significant (F(1,171) = 2.589, p = 0.008, $\eta^2_p = 0.120$), driven by relatively lower adaptation in the two anterior portions than the eight posterior portions ($t(174) = 4.536, p < 0.001$); the strength of adaptation was very close across the eight posterior portions. Critically, the interaction between cue type and portion was not significant ($F(9,171) = 1.010, p = 0.415, \eta^2_p = 0.050$). The main effect of cue type was not significant ($F(1,19) = 0.046, p = 0.833, \eta^2_p = 0.002$). None of the effects involving environment were significant ($Fs < 2.6, ps > 0.1, \eta^2_s < 0.15$). These results mean that i) overall, adaptation effects were rather distributed across a large part of RSC (i.e., 80% of the RSC towards its posterior end), and ii) adaptation change along the long axis of RSC was similar between the cue types.

To summarize, the univariate analyses conducted in participants’ native brains revealed no positive evidence for cue-specificity of the positional coding in RSC.

**Multivariate analysis.** The preceding univariate analyses, both in the standard space and the native space, revealed no significant differences or commonalities between landmarks and self-motion cues in adaptation. It is well-documented that fMRI univariate analyses are relatively limited in statistical power (Norman et al., 2006), because fine-grained spatial information across voxels is blurred and potential contributions from voxels with sub-threshold signals are ignored. To address these limitations, we adopted the multivariate analysis, which offers greater statistical power by overcoming the limitations of the univariate analysis. Moreover, it is possible that the underlying neural units coding positional information for different cue types are spatially intermixed across the entire region at a relatively high frequency, a pattern that detectable only through the multivariate approach.

To iterate, in the multivariate analysis, we assessed the similarity of the multi-voxel adaptation patterns (Figure 8a; Methods), i.e., we determined whether voxels showing higher adaptation for one cue also showed higher adaptation for the other cue. Specifically, we derived an adaptation pattern distinction score, which was quantified as within-cue similarity (cross-validated Pearson correlation between adaptation vectors of the same cue type) minus between-cue similarity.
(cross-validated Pearson correlation between adaptation vectors of different cue types) (Walther et al., 2016). The adaptation pattern distinction score was then tested against zero with a one-sided t test, as we expected the adaptation pattern to be more similar within the same cue type than between different cut types. A pattern distinction score significantly greater than 0 would indicate that the across-voxel adaptation pattern was distinct between the two cue types. Given the preceding results showing that the adaptation in RSC for landmarks was predominately driven by location identity, we adopted the location-identity-based adaptation for landmarks to increase sensitivity of the following statistical analyses.

First, we assessed cue-specificity/generalizability of positional coding while averaging across environments (Shine et al., 2019), because ‘environment’ served as a secondary factor in the experimental design and the preceding results showed no significant influences of this factor. As shown in Figure 8b, since the within-day pattern distinction score was significantly greater than the between-day distinction score (t(19) = 2.825, p_{1-tailed} = 0.011, BF_{10} = 4.799^g_1; gray bars), we tested them separately. The within-day pattern distinction score was significantly greater than 0 (t(19) = 2.885, p_{1-tailed} = 0.005, BF_{10} = 10.625^g_2; gray bar), because the within-cue similarity was significantly positive (t(19) = 2.708, p_{1-tailed} = 0.007, BF_{10} = 7.694^g_3; light blue bar) while the between-cue similarity was not (t(19) = -0.807, p_{1-tailed} = 0.779, BF_{10} = 0.141^g_4; salmon bar). In other words, while the adaptation pattern was stable for a given cue type, it differed between the two cue types. In contrast, the between-day pattern distinction score was not significantly greater than 0 (t(19) = -1.145, p_{1-tailed} = 0.867, BF_{10} = 0.120^g_5; gray bar).

To exclude the possibility that the aforementioned cue-specificity finding was solely driven by one of the two environments, we examined the two environments separately. The two environments showed a consistent pattern of results. In the nature environment (Figure 8c), the within-day adaptation pattern distinction score was significantly greater than 0 (t(19) = 1.915, p_{1-tailed} = 0.035, BF_{10} = 2.035^g_1; gray bar), because the within-cue similarity was significantly positive (t(19) = 2.611, p_{1-tailed} = 0.009, BF_{10} = 6.474^g_2; light blue bar) while the between-cue similarity was not (t(19) = 0.086, p_{1-tailed} = 0.466, BF_{10} = 0.248^g_3; salmon bar). In contrast, the between-day pattern distinction score was not significantly greater than 0 (t(19) = -0.354, p_{1-tailed} = 0.636, BF_{10} = 0.182^g_4; gray bar). Similarly, in the city environment (Figure 8d), the within-day pattern distinction score was significantly greater than 0 (t(19) = 2.022, p_{1-tailed} = 0.029, BF_{10} = 2.406^g_5; gray bar), because the within-cue similarity was significantly positive (t(19) = 1.933, p_{1-tailed} = 0.034, BF_{10} = 2.093^g_6; light blue bar) while the between-cue similarity was not (t(19) = -0.782, p_{1-tailed} = 0.778, BF_{10} = 0.142^g_7; salmon bar). In contrast, the between-day pattern distinction score was not significantly greater than 0 (t(19) = -1.092, p_{1-tailed} = 0.856, BF_{10} = 0.123^g_8; gray bar). Together, these results mean that in both environments, within the
same scanning day, the adaptation pattern was stable for a given cue type but differed between different cue types.

To characterize the anatomical distribution of cue-specific adaptation in RSC, we segmented RSC into ten equally-sized portions based on the dominant connectopy (Figure 8e), as described previously. We then assessed the contribution of each RSC portion to the within-day adaptation pattern distinction score by leaving it out from the calculation (i.e., the jackknife procedure). The resulting scores were subjected to a repeated measure ANOVA test, with portion as the independent variable. The main effect of portion was not significant ($F(9,171) = 0.571, p = 0.820, \eta_p^2 = 0.029$), meaning comparable contributions among the ten portions to the overall adaptation pattern distinction score. Interestingly, this finding contrasts with the earlier finding of lower univariate-mass adaptation effects in the two anterior portions compared to the eight posterior portions of RSC, meaning that portions lower in adaptation contributed as comparably to discriminating different cue conditions as other portions. Together, our results suggest that the positional coding within RSC was rather anatomically distributed, probably with neural units coding positional information for different cue types intermixed at a relatively high spatial frequency.

Our task design also allowed us to evaluate whether adaptation patterns were specific or generalizable between different environments for each cue type, although this was not our main interest of inquiry. For completeness, we compared adaptation patterns between different environments for each cue type. As shown in Figure 8f, in the landmark condition, the adaptation pattern distinction score within the same day was not significantly greater than 0 ($t(19) = 0.226, p_{1-tailed} = 0.588, BF_{10} = 0.198$), mainly due to the fact that the between-environment adaptation pattern similarity was significantly greater than 0 ($t(19) = 2.604, p_{1-tailed} = 0.009, BF_{10} = 6.400$). This result means that the adaptation pattern was significantly correlated between the two environments, indicating environment-independent spatial representations for landmarks. On the contrary, as shown in Figure 8g, in the self-motion condition, the adaptation pattern distinction score within the same day was significantly greater than 0 ($t(19) = 2.411, p_{1-tailed} = 0.013, BF_{10} = 4.564$), meaning distinct adaptation patterns between environments; this result was mainly driven by the within-environment adaptation similarity score being significantly greater than 0 ($t(19) = 2.655, p_{1-tailed} = 0.008, BF_{10} = 7.004$).

To summarize, we observed distinct voxel-to-voxel adaptation patterns between landmarks and self-motion cues in RSC: adaptation patterns were correlated within the same cue type but uncorrelated between different cue types. This effect occurred within the same scanning session and was regardless of the environment in which these cues were experienced. In addition, this cue-specific
positional coding within RSC seemed to be anatomically distributed across the region. Intriguingly, while the adaptation pattern was similar between environments for landmarks, it differed between environments for self-motion cues. This finding, however, does not undermine our interpretation of the main finding regarding distinct adaptation patterns between cue types. Since adaptation patterns were uncorrelated between cue types in each environment in the first place, the mean adaptation patterns averaged across environments would remain uncorrelated between cue types, regardless of whether the adaptation patterns are correlated or uncorrelated between environments for each cue type. Instead, this finding indicates that our multivariate analysis is sensitive to both the specificity and commonality in neural representations across experimental conditions. Together, our results demonstrate that spatial representations in RSC were cue-specific and were sensitive to the physical features of the spatial inputs.

Summary. While univariate analyses did not reveal any significant differences or commonalities in adaptation between cue types, the more sensitive multivariate analysis unveiled cue-specific positional coding in RSC, meaning that the voxel-to-voxel adaptation pattern was distinct between the cue types. These findings indicate that the underlying neural units responsible for encoding positional information for different cue types are probably intermingled at a relatively high spatial frequency in RSC.

Notably, our results collectively suggest a rather distributed arrangement of spatial representations across RSC. First, while the univariate analysis failed to uncover noticeable differences between cue conditions in adaptation, the multivariate analysis revealed significant differences in voxel-to-voxel adaptation pattern between cue types. Such a scenario typically occurs when the neural representations are spatially distributed across the brain region. Second, the eight posterior portions of RSC exhibited greater adaptation compared to its two anterior portions, yet the magnitude of adaptation across these eight posterior portions was very similar. This finding suggests that the neural representations are widely distributed throughout at least 80% of the RSC volume. Finally, no discernible differences were observed among the ten portions in their contributions to the cue-specific multi-voxel adaptation patterns, indicating that even the two anterior portions showing weaker adaptation contributed equally to discriminating cue conditions as the eight portions showing greater adaptation.

Control analyses
Compared to our previous study (Chen et al., 2019), one important advantage of the current paradigm is that it allowed us to evaluate whether the adaptation-based spatial coding was truly allocentric for each cue condition, by dissociating the length of the path leading to the test location and the allocentric position of the test location, since the starting position of the passive movement was randomized on a trial-by-trial basis for each cue type. In addition, as in our previous study, we also considered potential confounding influences of response adaptation, temporal distance, and passive movement. Given the preceding results showing that the adaptation in RSC for landmark was predominately driven by location identity, we adopted the location-identity-based adaptation for landmarks to increase sensitivity of the following statistical analyses.

To preview, we found that spatial coding in RSC for both cue types reflected allocentric positions of the test locations, and was not confounded by the aforementioned factors. In contrast, for the spatial coding in PHC for self-motion cues, allocentric location could not be unambiguously disentangled from path length and response.

**Path length.** To investigate whether the adaptation effects in RSC reflected path length or allocentric positions of the test locations, we directly compared these two variables by including both the allocentric-location-defined and the path-length-defined parametric regressors in the same first-level GLM (Mumford et al., 2015). For example, if the participant travelled 10 meters to Loc3 and 8 meters to Loc 4 on two successive trials, then the path-length-defined parameter has a value of |10-8| = 2m, whereas the location-defined parameter has a value of 4m for self-motion cues and 1 (different locations) for landmarks. In other words, path-length-based adaptation means that brain activation for the current trial is proportional to the absolute difference in path length between two successive trials.

In RSC, the unique contribution of path length was not significant for either cue type (landmark, t(19) = 1.185, p_{1-tailed} = 0.125, BF\textsubscript{10} = 0.430 \textsuperscript{1}; self-motion, t(19) = 1.374, p_{1-tailed} = 0.093, BF\textsubscript{10} = 0.525 \textsuperscript{2}), after accounting for location. On the contrary, the unique contribution of allocentric location was significant for both cue types (landmark, t(19) = 2.980, p_{1-tailed} = 0.004, BF\textsubscript{10} = 12.694 \textsuperscript{3}; self-motion, t(19) = 1.929, p_{1-tailed} = 0.034, BF\textsubscript{10} = 2.102 \textsuperscript{4}), after accounting for path length.

In PHC, in the self-motion condition, the unique contribution of location to adaptation was not significant after accounting for path length (t(19) = 0.464, p_{1-tailed} = 0.324, BF\textsubscript{10} = 0.342 \textsuperscript{1}), although the path-length-based adaptation was not significant itself (t(19) = 1.183, p_{1-tailed} = 0.126, BF\textsubscript{10} = 0.739 \textsuperscript{2}).
Given that the trial sequences were designed based on allocentric positions of the test locations to maximize the relative detection power in the first place (DP_{rel}; Aguirre et al., 2011), we evaluated whether differential detection power could have led to the observed dominance of allocentric location in adaptation (Extended Data 1, Section 1.7). As expected, the relative detection power was significantly greater for allocentric location than path length (F(1,19) = 9.184, p < 0.001, \eta_p^2 = 0.326), but the magnitude of the difference was minimal (mean DP_{rel} = 64.2% vs. 60.6%, mean difference = 3.6%). This suggests that the differential adaptation effects associated with allocentric location and path length are unlikely to have been caused by differences in detection power.

In brief, these results indicate that adaptation effects for both cue types in RSC predominantly reflected neural coding for allocentric location and were not confounded by the path to the test location. In contrast, the adaptation effect in PHC for self-motion cues could not be disentangled from path length.

**Response adaptation.** Although our task design ensured that choosing a given test location was not associated with a consistent motor behavior (Methods), it is important to examine whether the adaptation was confounded by possible response-related adaptation based on participants’ subjective recognition of the test location. Trial-specific subjective response – reflecting a participant’s belief of the currently occupied location – allowed for a location-wise dissociation between objective location and subjective response. We directly compared location and response by including the location-defined parametric regressor and the response-defined parametric regressor in the same first-level general linear model (Mumford et al., 2015).

In RSC, the unique contribution of response was not significant in either cue condition, after accounting for location (landmark: t(19) = 0.117, p_{1-tailed} = 0.454, BF_{10} = 0.254^m1; self-motion: t(19) = -0.781, p_{1-tailed} = 0.778, BF_{10} = 0.143^m2). In contrast, the unique contribution of location was significant in both cue conditions (landmark, t(19) = 2.093, p_{1-tailed} = 0.025, BF_{10} = 2.694^m3; self-motion, t(19) = 2.137, p_{1-tailed} = 0.023, BF_{10} = 2.892^m4), after accounting for response. These results indicate that objective location rather than subjective response was the driving factor of the adaptation effects in RSC for both cue types.

In PHC, in the self-motion condition, the unique contribution of location was not significant after accounting for response (t(19) = 0.583, p_{1-tailed} = 0.283, BF_{10} = 0.383^n1), although the response-based adaptation was not significant itself (t(19) = 1.118, p_{1-tailed} = 0.139, BF_{10} = 0.683^n2).
Although the location-defined trial sequences had significantly higher empirical \( \text{DP}_{\text{rel}} \) than response-defined sequences as expected (\( F(1,19)= 19.007, p < 0.001, \eta^2 = 0.500 \)), the magnitude of the difference was negligible (mean \( \text{DP}_{\text{rel}} = 64.2\% \) vs. 63.1\%). This indicates the differences in adaptation associated with location and response were not caused by differences in detection power.

Finally, we conducted the voxel-wise analysis to investigate adaptation in the entire-volume (Extended Data 1, Figure E7). In posterior cingulate areas (including RSC proper and the putative retrosplenial complex), adaptation appeared to be stronger when based on location than response in both cue conditions. This trend also existed in other brain regions, e.g., precuneus, calcarine, and angular gyrus.

However, one potential limitation of this control analysis pertains to the high behavioral accuracy exhibited by our participants, particularly in the landmark condition. The dissociation between objective location and subjective response was positively proportional to the number of mistakes committed by participants. Nonetheless, we consider the results obtained from this analysis valid, for the following three reasons. First, the reliability of beta estimates for the GLM regressors is determined by the correlations between the parametric regressors modeling the location-based adaptation and the response-based adaptation, which turned out to be generally lower than the behavioral accuracy levels (Extended Data 1, Figure E8). This discrepancy holds particularly true for the landmark condition, where the parametric regressors modeled location identity instead of continuous inter-location distance (Figure E8a). Second, the robustness of beta estimates of the GLM regressors was bolstered by the large number of trials included in the current task design, which could mitigate adverse effects of multicollinearity to some extent. Third, the pattern of results was consistent across both cue types. Nevertheless, we acknowledge that future investigations employing more challenging tasks are needed to validate our findings.

**Temporal distance.** Neural adaptation is highly sensitive to the temporal intervals between successive events (Barron et al., 2016). In the paradigm used in our previous study (Chen et al., 2019), we demonstrated that adaptation effects in EC were not confounded by the temporal delay between successive trials, because the two parameters were minimally correlated in the first-level GLM. Here, we conducted the same analysis to contrast these two variables by including the parametric modulation regressors defined by each of them in the same first-level GLMs (Mumford et al., 2015). For example, if the participant visited Loc1 and Loc2 in two successive trials, and the temporal delay between the two location occupation events was 8 second, then the temporal-distance-defined
parameter had a value of 8, and the location-defined parameter had a value of 4m in self-motion trials and 1 (= different locations) in landmark trials.

Same as in our previous study, the location-defined parameter and the temporal-distance-defined parameter had minimal correlations with each other \((|rs| < 0.1, ps > 0.1, n = 256)\). Furthermore, in RSC, the unique contribution of location was significant after accounting for temporal distance for both cue types (landmark, \(t(19) = 3.399, p_{1\text{-tailed}} = 0.002, BF_{10} = 28.206^{p1}\); self-motion, \(t(19) = 3.082, p_{1\text{-tailed}} = 0.003, BF_{10} = 15.359^{p2}\)). Conversely, after accounting for location, the unique contribution of temporal distance was not significant in the landmark condition \((t(19) = 1.171, p_{1\text{-tailed}} = 0.128, BF_{10} = 0.728^{p3})\), and was significant in the self-motion condition (with one outlier winsorized, \(t(19) = 2.044, p_{1\text{-tailed}} = 0.028, BF_{10} = 2.488^{p4}\)). However, unlike location, the unique contribution of temporal distance self-motion cues was significant in all the other ROIs \((p_{1\text{-tailed}} < 0.04, BF_{10} > 2)\), except the right aIEC \((t(19) = 1.287, p_{1\text{-tailed}} = 0.107, BF_{10} = 0.841^{p5})\). Together, these results indicate that the positional coding observed in RSC was not confounded by the temporal distance between successive location occupation events.

In PHC, in the self-motion condition, the unique contribution of location was significant after accounting for temporal distance \((t(19) = 1.961, p_{1\text{-tailed}} = 0.032, BF_{10} = 2.186^{q1})\), as was the unique contribution of temporal distance \((t(19) = 2.309, p_{1\text{-tailed}} = 0.016, BF_{10} = 3.841^{q2})\).

In brief, all the adaptation effects observed in RSC and PHC were not confounded by temporal distance between successive location occupation events, because our task design ensured that temporal distance and inter-location relation were largely dissociated and minimally correlated with each other. Interestingly, there existed neural coding of temporal distance for self-motion cues in most of our ROIs after accounting for location; however, the interpretation of this phenomenon was not pursued here.

**Passive movement phase.** In the location identification task, the location occupation phase – which was used to assess adaptation-based positional coding and was rendered the same for the two cue types – was preceded by a passive movement, during which the sensory inputs differed between the cue types. Given the slow temporal dynamics of the hemodynamic response, it is possible that the adaptation effect measured at the location occupation phase could have reflected effects in the passive movement stage.

To address this issue, in our main analyses, to account for potential influences of the passive movement phase that preceded the location occupation phase, the passive movement phase was...
modeled in the first-level GLMs (Methods). Here, we conducted additional analyses in which the passive movement phase was not modeled in the GLM, and found that the adaptation results remained unchanged: RSC showed significant adaptation for landmarks, $t(19) = 3.624, p_{1\text{-tailed}} < 0.001$, $BF_{10} = 43.706^{13}$; RSC showed significant adaptation for self-motions, $t(19) = 3.026, p_{1\text{-tailed}} = 0.003, BF_{10} = 13.818^{12}$; PHC showed significant adaptation for self-motion cues, $t(19) = 2.767, p_{1\text{-tailed}} = 0.006, BF_{10} = 8.572^{11}$; when comparing the voxel-to-voxel distributed pattern of adaptation between the cue types, the within-day adaptation distinction score was significantly greater than 0 in RSC ($t(29) = 2.694, p_{1\text{-tailed}} = 0.007, BF_{10} = 7.511^{16}$), indicating cue-specific spatial representations in this region.

To thoroughly assess how previous navigation experiences influence location-based adaptation during the location occupation phase, we created another GLM, in which we extended the regressors that represent the "movement" phase to encompass the entire navigation process, i.e., including phases 1, 2, and 3. Our primary findings remained stable with this revised GLM. First, the univariate adaptation analyses showed that RSC contained significant categorical location-identity coding in the landmark conditions ($t(19) = 3.462, p_{1\text{-tailed}} = 0.001, BF_{10} = 31.856^{15}$) and continuous inter-distance coding in the self-motion condition ($t(19) = 3.149, p_{1\text{-tailed}} = 0.003, BF_{10} = 17.435^{16}$). PHC showed significant adaptation for self-motion cues ($t(19) = 2.836, p_{1\text{-tailed}} = 0.005, BF_{10} = 9.724^{17}$).

Second, the multivariate analysis showed that in RSC, the within-day adaptation pattern distinction score was significantly greater than 0 ($t(19) = 2.508, p_{1\text{-tailed}} = 0.011, BF_{10} = 5.400^{18}$), which was driven by the within-cue pattern similarity being greater than 0 ($t(19) = 2.721, p_{1\text{-tailed}} = 0.007, BF_{10} = 7.880^{19}$). These results mean that the passive movement phase should not influence the adaptation-based positional coding assessed during the location occupation stage, as whether modeling the passive movement stage or not in the GLM did not affect the results. This is expected, because same as our previous study (Chen et al., 2019), the current task design ensured minimal correlation between the event regressor modeling the passive movement phase and the parametric regressor modeling the inter-location spatial relation for the location occupation phase in the first-level GLM ($|rs| < 0.01$).

In brief, the adaptation effects observed in RSC and PHC should not have been confounded by the passive movement phase preceding the location occupation phase.

Successful navigation involves brain regions different from Chen et al. (2019)

So far, the current study exhibited a different pattern of results on adaptation from our previous study (Chen et al., 2019). To further illustrate potential differences between the two studies, we assessed whether the ROIs was involved in the navigation task by exhibiting the successful navigation effect
(Chrastil et al., 2015; Pessoa et al., 2002), i.e., stronger activation in correct trials than incorrect trials (Methods).

As shown in Figure 9, the ROI-based analysis revealed significant successful navigation effects in RSC (F(1,19) = 17.267, p = 0.001, ηp² = 0.476), PHC (F(1,19) = 6.282, p = 0.021, ηp² = 0.248), and the left EC (with one outlier winsorized, F(1,19) = 4.765, p = 0.042, ηp² = 0.201). These brain areas were more strongly activated in correct trials compared to incorrect trials. Other ROIs did not show significant successful navigation effects (Fs < 1.5, p > 0.2, ηp² < 0.08). We did not observe any main effects of cue type (Fs < 3, p > 0.11, ηp² < 0.13) or interaction effects between cue type and correctness (Fs < 0.7, p > 0.4, ηp² < 0.04).

In brief, the results showed stronger recruitment of RSC, PHC, and the left aEC during successful trials compared to failed trials, underscoring their crucial role in facilitating accurate navigation. It’s worth noting that different from the current study, our previous study (Chen et al., 2019) observed that all the MTL regions and RSC exhibited significant successful navigation effect (Table E3). This discrepancy in successful navigation effect further indicates that dissimilar neural mechanisms were engaged in the navigation processes in our two studies.

DISCUSSION

The current study investigated whether landmark-based navigation and path integration recruit cue-specific or cue-independent spatial representations in the human brain, using a modified version of the simple navigation task employed in our previous investigation (Chen et al., 2019). The results showed that: first, RSC displayed adaptation-based positional coding for both landmarks and self-motion cues; second, the positional coding in RSC primarily reflected allocentric spatial position rather than the path to the spatial location, indicating authentic allocentric spatial representations; third, the voxel-to-voxel distributed pattern of adaptation differed between the cues, suggesting cue-specific positional coding. In addition to RSC, we also observed positional coding for self-motion cues in PHC, albeit smaller in magnitude and not dissociable from the path to the spatial location. Although we did not replicate our previous observation of adaptation-based positional coding in EC subregions under the current new experimental conditions, the brain regions contributing to successful navigation also differed from those observed in our previous study, indicating overall differential neural mechanisms between the two studies. In brief, to the best of our knowledge, the current study provides the first evidence for the existence of cue-specific spatial representations in human RSC during the performance of a navigation task within the same spatial context. Furthermore, the current study underscores the dependency of spatial representations in the brain on specific experimental setups.
The following discussion will be organized as follows: first, we will discuss the positive findings of adaptation-based positional coding in RSC and PHC. Second, we will analyze the key methodological differences between the current study and our previous study (Chen et al., 2019) to understand the discrepancies in the recruited neural mechanisms.

**Allocentric positional coding in RSC**

The central finding of the current study is the adaptation-based positional coding in RSC for both cue types. This finding aligns with many studies in humans and non-human animals that have implicated RSC in landmark-based navigation and path integration. For instance, human neuroimaging studies have demonstrated that RSC encoded permanence of visual landmarks (Auger et al., 2015), that RSC activity was modulated by the navigator’s instantaneous Euclidean distance from the path origin in a loop-closure path integration task (Chrastil et al., 2015), and that RSC activity encoded location-identity for spatial locations defined by landmarks in real-world environments (Morgan et al., 2011). Similarly, studies in rodents have shown that firing patterns of retrosplenial place-cell-like neurons were influenced by both visual and self-motion information (Fischer et al., 2020; Mao et al., 2020), and that RSC lesions caused deficits in both path integration (Elduayen & Save, 2014) and landmark-based navigation (Clark et al., 2010). Collectively, these findings provide strong evidence that RSC processes both landmark and self-motion information during spatial navigation (Todd & Bucci, 2015), which is consistent with RSC’s role as a polymodal midline structure receiving inputs from various (sub-)cortical areas that process different sensory inputs (Kobayashi & Amaral, 2003; Parvizi et al., 2006; Vann et al., 2009).

While broadly consistent with previous research, our study offers novel evidence that RSC mediates spatial representations in both navigation modes within in the same task. Furthermore, spatial coding in RSC was not confounded by the length of the path taken by the participant to reach the location, meaning that it reflects a genuine positional code of allocentric locations. This finding aligns with the recent discoveries of place-cell-like neurons in RSC, which, similar to hippocampal place cells, fire when a rodent occupies a specific location in the environment (Mao et al., 2017; Miller et al., 2021). Finally, the navigation task employed in the current study solely involved positional estimation on a one-dimensional linear track without requiring head direction estimation, emphasizing RSC’s role in positional processing without angular computations (Chrastil et al., 2016; Mao et al., 2017, 2020). This finding complements the well-documented role of RSC in head direction representations (Marchette et al., 2014; Shine et al., 2016; Taube, 1998).
While RSC exhibited positional coding for both landmarks and self-motion cues, our results showed different representational formats between them. For landmarks, positional coding primarily distinguished between the same and different locations, indicating neural coding of location identity. In contrast, RSC’s positional coding in the self-motion condition reflected inter-location distance in a continuous manner. Notably, the spatial distance information contained in RSC activity for self-motion cues was precise enough to allow for accurate recovery of the original physical space.

Why should the representational format differ between the two cue types? One possible explanation is that the underlying neuronal tuning curves associated with test locations were sharper for landmarks than self-motion cues (Fang et al., 2007). This explanation is in line with our behavioral finding that participants performed better with landmarks than self-motion cues, because sharper tuning curves typically lead to better discrimination among locations. When tuning curves for individual locations are very sharp, as hypothesized for landmarks, there is complete neural overlap when successive locations are the same. However, this overlap quickly reduces to minimal levels when the successive locations differ, resulting in location-identity coding. In contrast, when tuning curves are broader, as hypothesized for self-motion cues, the neural overlap between successive locations decreases only gradually with increasing inter-location distance, resulting in inter-location-distance coding.

The tuning curve explanation relates the adaptation effect in RSC to participants’ overt behavioral performance, which may appear contradictory to our finding that the adaptation effect was driven by the stimulus input (i.e., objective location) rather than the retrieved memory reflected in participants’ behavior (i.e., subjective response). However, this contradiction is not necessarily valid, as stimulus input and behavioral performance are intertwined, e.g., high-quality stimulus can facilitate memory retrieval. It is conceivable that different parameters of the presumed tuning curves contribute to different aspects of the adaptation effect and participants’ behavior. The means of the tuning curves dictate their positions in space, determining whether objective location or subjective response fits the adaptation effect better. Meanwhile, the standard deviations of the tuning curves denote the precision of the sensory information, influencing the format and magnitude of adaptation, which, in turn, relates to behavioral accuracy and is likely impacted by memory stage.

Nevertheless, sharp tuning curves alone may not fully account for the location-identity coding for landmarks in RSC. First, previous fMRI adaptation studies have reported that with very high behavioral accuracy, RSC can exhibit either continuous inter-location-distance coding (Kim & Maguire, 2018; Sulpizio et al., 2014) or location-identity coding (Morgan et al., 2011). Second, our previous study reported continuous inter-location-distance coding for both landmarks and self-motion cues in.
EC in terms of adaptation, when behavioral accuracy was higher for landmarks than self-motion cues (Chen et al., 2019), albeit still considerably lower than the current study (Extended Data 1, Figure E3).

Finally, these two different formats of adaptation-based neural coding have been observed in different brain regions in the same experiment (Fang et al., 2007; Morgan et al., 2011). We speculate that besides behavioral accuracy, other factors such as intrinsic neuronal response properties of the brain region may influence the adaptation format. For instance, location-identity coding in RSC, which is probably driven by sharp tuning curves, might reflect RSC’s crucial role in the spatial processing of landmarks – RSC might be particularly tuned to extracting precise spatial information from landmarks to support discrete landmark-based navigation (Auger et al., 2012; Fischer et al., 2020; Yoder et al., 2011). Moreover, our explicit instruction to retrieve the identities of individual test locations might have emphasized the extraction of discrete location-identity information, at least for landmarks.

Furthermore, the tuning curve explanation should be taken with caution, given the complex relationship between fMRI adaptation and neuronal activity (Larsson et al., 2016). Further investigation is needed to fully elucidate the factors influencing the format of spatial representation in various brain regions.

In addition to RSC, we also observed positional coding in PHC for self-motion cues. This finding is consistent with previous research that has demonstrated the involvement of PHC in path integration based on optic flow (Chrustil et al., 2015, 2016). However, unlike RSC, we could not determine this coding in PHC to be truly allocentric, since location adaptation was not dissociable from adaptation to path length.

Positional coding in RSC is cue-specific

Crucially, beyond showing that RSC activity contained allocentric positional information extracted from both landmarks and self-motion cues, our study also revealed the positional coding to be cue-specific rather than cue-independent, because the distributed pattern of adaptation was distinct between the two cue types. This finding suggests the existence of distinct underlying neural units that code spatial information for different cue types (Norman et al., 2006).

It is important to keep in mind that in our task, the sole difference between different cue conditions was the type of spatial information available. Therefore, cue-specific spatial representations in RSC were not confounded by extrinsic factors such as task requirements or reward setups (Radvansky et al., 2021), but rather reflected the effects of spatial cues used for navigation. Furthermore, the cue-specific adaptation-based positional coding in RSC was mainly driven by
correlated distributed adaptation patterns within the same cue type, which indicates that the
significant univariate adaptation effects in RSC are unlikely to be false positive results. This is because
pure noise should be independent across different fMRI scanning runs, resulting in zero voxel-to-voxel
correlations across runs (Walther et al., 2016).

Two related studies have investigated cue-specificity of spatial representations in RSC, even
though studies alike abound on the hippocampus (e.g., Geva-Sagiv et al., 2016; Markus et al., 1994;
Radvansky et al., 2021). The first study reported that the place-cell-like population vector coding of
spatial locations in the rodent RSC remained largely unchanged when the light was switched on versus
off, indicating cue-independent spatial representations (Mao et al., 2017). The second study is a
human fMRI study, which also reported cue-independent spatial representations in RSC, because
several readouts of brain activity (e.g. overall brain activity, inter-region functional connectivity
pattern, multi-voxel similarity of brain activation), did not differ between different virtual
environments learned with different degrees of body-based self-motion cues (Huffman & Ekstrom,
2019).

How can we reconcile the current finding of cue-specific spatial representations with these
two studies? First, a clear dissociation of the cues, as demonstrated in the cue-specific behavioral
accuracy profiles across test locations in the current study, may be critical for inducing cue-specific
representations. Specifically, we observed that in the landmark condition, behavioral performance
improved as the test location approached the landmark, whereas the opposite pattern emerged in
the self-motion condition. This cue-specific behavioral performance pattern can be attributed to the
fact that spatial precision of landmark-based navigation diminishes as the distance from the landmark
increases (Chamizo et al., 2006; Chen et al., 2019), whereas path integration becomes more prone to
noise as the navigator traverses the path away from its anchoring point – the starting position of
movement (Stangl et al., 2020). These findings align with previous research demonstrating a relative
independence of path integration and landmark-based navigation in behavioral studies (Chen et al.,
2017; Etienne et al., 1996), indicating that our cue dissociation manipulation successfully elicited
distinct navigational strategies with different spatial cues.

In this context, it is important to note that in the study by Mao et al. (2017), self-motion cues
were present both when the light was on and off, along with other possible uncontrolled cues (e.g.,
somatosensory and olfactory cues). Therefore, the observed cue-independent spatial representations
may have rather reflected the coding of certain common spatial information shared by different cue
conditions.
Second, experiencing the sensory information to retrieve locations from memory might be another key to evoking cue-specific representations. Unlike our on-line navigation task in which participants actually navigated with sensory information available within the virtual environment, Huffman & Ekstrom (2019) asked participants to imagine themselves occupying previously learned locations, without perceiving the actual sensory inputs that obviously differed between different cues.

Finally, we utilized fMRI adaptation to evaluate positional coding. It’s worth noting that fMRI adaptation often exhibits heightened sensitivity to the low-level physical characteristics of stimuli, as opposed to measures such as the representational similarity of activation vectors or the multi-voxel pattern analysis (MVPA) in general (Epstein et al., 2003; Epstein & Morgan, 2012; O’Connell et al., 2018). This observation aligns with our discovery of cue-specific location-based adaptation in RSC, because the sensory inputs evidently differed between cue types at a level lower than abstract positional representations. One plausible explanation for the stimulus-sensitivity of fMRI adaptation is that it might reflect the synaptic processing (Epstein & Morgan, 2012; Sawamura et al., 2006). However, the elusive relationship between BOLD signals and neuronal activity (Arthurs & Boniface, 2002), combined with the finding that BOLD signals generally correlate better with synaptic inputs than spiking outputs of neurons (Logothetis et al., 2001), leaves the precise reason for stimulus-sensitivity of fMRI adaptation unclear. Nevertheless, it is conceivable that fMRI adaptation interrogates different aspects of the underlying neural codes compared to other measures, such as univariate mass activation and multi-voxel activation pattern similarity in Huffman & Ekstrom (2019) and neuronal spiking activity in Mao et al. (2017). These methodological differences may explain the disparities between the current study and the two prior studies, highlighting the importance of employing complementary measurements to obtain a more complete picture of how the brain processes various spatial cues during navigation (Chen et al., 2022).

Distinct neural mechanisms between the current study and Chen et al. (2019)

Despite employing similar task paradigms and identical MRI scanning sequences to contrast landmarks and self-motion cues in spatial navigation, the current study yielded divergent fMRI results from our previous investigation in terms of both adaptation and successful navigation effects (Chen et al., 2019). Regarding adaptation, while our previous study observed adaptation in the right EC, the present study only revealed adaptation in RSC and PHC, but no adaptation in EC. The absence of significant adaptation in EC could not explained by signal quality, as the temporal signal-to-noise ratio in EC was actually lower in our previous study (~11.3) compared to the current study (~13.5; Figure
Regarding successful navigation, the overall participation of MTL was substantially reduced in the current study, whereas the participation of RSC remained comparable between the two studies.

These discrepancies can be attributed to two notable methodological differences between our two studies. First, compared to Chen et al. (2019), participants in the current study were in a relatively late memory stage during functional scanning: participants initially showed learning effects on the Pre-scan day, reaching a performance plateau that remained stable throughout the two sessions of functional scanning (Figure E2). This finding was likely due to two factors: first, participants were trained intensively on a separate day prior to the scanning; second, participants’ spatial memories probably had been consolidated by sleep between the scanning sessions. In contrast, participants in our previous study did not exhibit any learning effects, indicating they were fixed in an early memory stage (Figure E3). There is abundant evidence indicating that memories transition from MTL to cortical areas over time (Alvarez & Squire, 1994). Prior spatial navigation studies have demonstrated a shift in the locus of spatial representations from the hippocampus to RSC over time, as hippocampal activity reflects the learning rate, whereas the retrosplenial activity is associated with the fidelity of acquired spatial knowledge (Diersch et al., 2021; Wolbers & Büchel, 2005). Therefore, our findings of reduced involvement of MTL in navigation task completion and strong spatial representations in RSC might be attributable to the relatively late memory stage.

The second critical difference was the longer temporal intervals between location occupation events in the current study compared to Chen et al. (2019) (mean interval ~7.2 s vs. ~3 s). This difference stemmed from the wider spacing of test locations in the current study, while movement speeds remained unchanged. FMRI adaptation is highly sensitive to temporal intervals; longer ones may attenuate neuronal adaptation (Barron et al., 2016). However, since varying temporal intervals should not affect participants’ behavioral performance and hence the involvement of brain regions in accurate navigation, temporal intervals are unlikely to be the sole factor contributing to the discrepancies between the two studies.

In summary, our previous observation of adaptation-based spatial coding in the entorhinal subregions but not in RSC and other MTL regions cannot be generalized to the current experimental context, highlighting the dynamic and complex nature of spatial information processing in the brain. Future studies are warranted to elucidate the factors influencing neural coding during different navigation modes.

Limited involvement of hippocampus
We observed little hippocampal involvement in the positional coding. While we identified one cluster showing adaptation to landmarks (Figure E4, a.2) and one cluster showing successful navigation effect extending into the hippocampus (Figure E9c), their peak voxels did not reside within the hippocampus according to AAL template denotation. These results echo with our previous study, where a cluster showing adaptation to self-motion cues extended into the hippocampus, but its peak voxel fell within the thalamus (Chen et al., 2019, Figure 5).

Interestingly, although the univariate analysis did not reveal adaptation for either cue type in the hippocampus (Figure 4b), the multivariate analysis revealed cue-specific adaptation patterns in this region (Figure E12). Additionally, the hippocampus showed strong functional connectivity with RSC (Figure E13). These results implicate the potential existence of weak positional coding in the hippocampus (Norman et al., 2006).

In summary, with only one spatial cue type for navigation, the hippocampus appears to exhibit limited positional coding. This finding aligns with rodent studies indicating that robust positional coding in the hippocampus requires the integration of different spatial cues (Brun et al., 2008; Lu et al., 2013).

CONCLUSIONS

To conclude, our study aimed to address a fundamental question in spatial navigation: Do landmark-based navigation and path integration utilize shared or separate spatial representations in the brain? We tested the generalizability of our previous finding of spatial coding in the right entorhinal cortex under a different experimental condition. Although not replicating this previous finding in the new paradigm, we discovered strong and cue-specific allocentric spatial representations in RSC. Further investigations should clarify the elements that impact neural encoding of spatial information during different navigation modes.

REFERENCES


Video
Title: Demo of the experimental environments and tasks, related to Figure 1 and the section ‘Stimuli and navigation task’ in Methods. Demo of the learning trials starts at 0’0” and ends at 1’24”. Demo of the location identification task (i.e., test) starts at 1’25” and ends at 2’48”.

Video file: Learning_and_location_identification_task_demo.mp4
There were two different virtual environments (left): nature (upper panel) and city (lower panel). The two environments shared the same object layout on the linear track (left). There were arrows, four differently colored balls on poles, and a tree on the linear track. The four balls were positioned at the four test locations, i.e., Loc1, Loc2, Loc3, and Loc4. To improve visibility, we used three identical arrows positioned above the ground to denote the same spatial position, meaning that the arrows vertically projected to the same position on the ground and only differed in height. The arrows, the tree, and the floor texture of the linear track had the same physical appearances but in different colors in the two environments. The four balls positioned at the test locations were the same but reversed in order in the two environments. The floor texture outside of the linear track also differed between the two environments. Displayed on the right are snapshots of the two environments, with the background environment, the linear track, the tree, the arrows, and the ball positioned closest to the arrows.

The time course of the location identification task. Here, the trial is depicted in the nature environment. Each trial had six phases. In phase 1 ‘start’, the participant was positioned at the starting location, which was randomized trial by trial based on a uniform distribution [−18 m, −4 m] (see Figure 1a, left). In phase 2 ‘movement’, the participant was passively transported to one of the four test locations. In phase 3, after arriving at the test location, the participant’s first-person perspective was smoothly turned down to vertically face the ground. In phase 4 ‘location occupation’, the participant’s perspective was fixed at the ground for four seconds. In phase 5 ‘response’, participant was required to identify the color of the ball positioned at that location within 20 second. In phase 6 ‘feedback’, feedback was provided, telling the participant whether the response was accurate, and, if incorrect, what the correct answer was. Note that the balls remained invisible throughout the trial, so that participants needed to recall from memory the color of the ball associated with the test location. In the landmark condition, the arrows were invisible, the tree was displayed, and the floor of the linear track remained blank. In the self-motion condition, the arrows were displayed, the tree was invisible, and the texture of the linear track was displayed. In both conditions, the background environment only appeared briefly at the beginning of the trial (= 0.7s), and disappeared once the passive movement started. The fMRI analyses focused on the 4-second location occupation period (i.e., phase 4), when the visual inputs were the same for both cue conditions.

Participants were familiarized with the virtual environments and trained in the location identification task on the first day (Pre-scan day). On the following two days (MRI_day1 & MRI_day2), they completed the location identification task while undergoing MRI scanning in the 7T scanner. In each scanning session, each of the four condition combinations was conducted for two runs, and the eight runs were counterbalanced with the Latin square design.

For full details of the virtual environments and the experimental tasks, see Methods and the video.
Figure 2. MRI acquisition and anatomical masks of regions of interests.

(a) MRI scanning and regions of interest. For an exemplary participant, the functional scan (in green) and the T2-weighted structural scan (in blue) are overlaid on the brain extracted from the T1-weighted structural scan.

(b) For an exemplary participant, the anatomical mask of retrosplenial cortex (RSC; in red) and the anatomical mask of hippocampus (in violet) are overlaid on the brain extracted from the T1-weighted structural scan.

(c) Manually segmented anatomical masks for regions in the medial temporal lobe (MTL) in one exemplary participant.

(d) Manually segmented anatomical masks for hippocampal subfields in one exemplary participant.


Figure 3. Behavioral results.

Behavioral accuracy is plotted as a function of cue type and test location in each experimental day.

Error bars represent ± S.E.

Figure 4. Adaptation in all ROIs.

(a) Adaptation in entorhinal subregions with inter-location-distance modelled.

(b) Adaptation in hippocampal subfields with inter-location-distance modelled.

(c) Adaptation in RSC, HIPP, PHC, and PRC with inter-location-distance modelled.

(d) Visualization of significant adaptation effects in RSC for both cue types and in PHC for self-motion cues.

The ROI’s activation was plotted as a function of inter-location distance.

Statistical outliers were highlighted in red circles, which were winsorized to the nearest inlier in statistical tests.


Figure 5. Contrasting inter-location-distance and location-identity in adaptation in RSC.

(a) Visualization of adaptation effect in RSC for landmarks. The ROI’s activation is plotted as a function of inter-location distance, same as Figure 4d (left, landmark).

(b) Disentangling inter-location-distance and location-identity in adaptation for landmarks. The total contribution and unique contribution of inter-location distance and location identity are plotted. The unique contribution represents the contribution of the variable after the other variable has been accounted for.

(c) The neural space reconstruction analysis. The multi-dimensional scaling analysis (MDS) and Procrustes analysis were applied to the normalized neural distance matrix calculated from trial-wise activation levels of
the brain region. The reconstructed neural space (red circles) is compared to the physical space (blue circles).
Significant results (p < 0.05) indicate resemblance of the neural space to the physical space.

Figure 6. Retrospenial clusters showing significant location-based adaptation.
The two clusters are rendered in the MNI template brain, viewed from the front (left) and the back (middle) in
the 3D brain, as well as in the sagittal view of the brain (right). The clusters are within the group-level anatomical
mask of RSC. The cluster-defining threshold is T > 3. The landmark cluster consists of 1029 voxels (blue), and the
self-motion cluster consists of 153 voxels (red). The adaptation reflects location identity for landmarks and inter-
location distance for self-motion cues.

Figure 7. Functional segmentation of RSC and location-based adaptation.
(a) Visualization of the gradient in RSC in the current study, based on the dominant connectopy.
(b) RSC was divided into ten equally-sized portions, based on the gradient shown in (a).
(c) fMRI adaptation for landmarks (location-identity-based) and self-motion cues (inter-location-distance-
based) for the ten retrosplenial portions, averaged across the nature environment and the city environment.
(d) fMRI adaptation for landmarks (location-identity-based) and self-motion cues (inter-location-distance-
based) for the ten retrosplenial portions, in the nature environment.
(e) fMRI adaptation for landmarks (location-identity-based) and self-motion cues (inter-location-distance-based)
for the ten retrosplenial portions, in the city environment.

Figure 8. Results of fMRI adaptation pattern similarity analysis.
(a) Setup of the fMRI adaptation pattern similarity analysis. The adaptation vectors were paired up to one
another, resulting in 2×2 = 4 different types of pairing: cue relation (within-cue vs. between-cue) × day
relation (within-day vs. between-day).
(b) Adaptation patterns are compared between cues, with the ‘environment’ factor averaged out. Adaptation
pattern similarity is plotted as a function of cue relation and day relation. The adaptation pattern distinction
score (within-minus-between, gray bars) equals to within-cue similarity (light blue bars) minus between-cue
similarity (salmon bars).
(c) Results in the nature environment, comparing adaptation patterns between cues.
(d) Results in the city environment, comparing adaptation patterns between cues.
(e) Assessing relative contributions of individual retrosplenial portions to the overall within-day adaptation
pattern distinction score, which corresponds to scores indicated by the gray bars in (b), (c), and (d). The left
panel shows RSC segmentation based on the gradient of the dominant connectopy, same as in Figure 7b. The
right panel shows the within-day adaptation pattern distinction score as a function of the left-out portion. The
scores were all significantly greater than 0 and did not differ from one another.
(f) Results for landmark cues, comparing adaptation patterns between the two environments.
(g) Results for self-motion cues, comparing adaptation patterns between the two environments.

Figure 9. Effects of successful navigation in all ROIs.
Brain activation is plotted as a function of cue type (landmark vs. self-motion) and navigation success (correct
vs. incorrect). Left aEC, RSC and PHC showed significant main effect of navigation success. Error bars represent
±SE.

Error bars represent ±SE. ‘*’ – p_{1-tailed/2-tailed} < 0.05, ‘**’ – p_{1-tailed/2-tailed} < 0.01, ‘+’ – p_{1-tailed/2-tailed} < 0.1.
### Table 1. Adaptation in all ROIs.

`P_{1-tailed}` represents the statistical significance one-tailed one sample t test on adaptation. In correspondence to Figure 4. Significant results are highlighted in bold. BF\textsubscript{10} represents the Bayes factor showing evidence for the alternative hypothesis over the null hypothesis. 'landmark#' represents when the statistical outlier was winsorized. 'landmark%' represents when location-identify was modeled in adaptation in RSC for the landmark condition. In all other cases, inter-location distance was modeled in adaptation.

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### Analysis of adaptation across retrosplenial portions

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### Comparing adaptation patterns between cue types, with environment averaged out

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### Comparing adaptation patterns between cue types, in each environment

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### Contributions of retrosplenial portions to cue-specific adaptation patterns

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</table>

### Comparing adaptation patterns between

<table>
<thead>
<tr>
<th></th>
<th>Distribution</th>
<th>Test</th>
<th>Effect</th>
<th>BF$_{10}$</th>
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</thead>
<tbody>
<tr>
<td>i1</td>
<td>Normally distributed</td>
<td>One-sided one sample t test</td>
<td>0.588</td>
<td>0.198</td>
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<tr>
<td>Environment</td>
<td>Distribution</td>
<td>Test</td>
<td>p Value</td>
<td>BF_{10}</td>
</tr>
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<td>-------------</td>
<td>--------------</td>
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<td>---------</td>
<td>---------</td>
</tr>
<tr>
<td>i2</td>
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<td>One-sided one sample t test</td>
<td>0.009</td>
<td>BF_{10} = 6.400</td>
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<tr>
<td>i3</td>
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<td>One-sided one sample t test</td>
<td>0.013</td>
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<td>i4</td>
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<td>0.008</td>
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</tr>
<tr>
<td>j1</td>
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<td>0.125</td>
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</tr>
<tr>
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<td>One-sided one sample t test</td>
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<tr>
<td>j3</td>
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<td>One-sided one sample t test</td>
<td>0.004</td>
<td>BF_{10} = 12.694</td>
</tr>
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<td>j4</td>
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<td>One-sided one sample t test</td>
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<td>k1</td>
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</tr>
<tr>
<td>k2</td>
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<td>One-sided one sample t test</td>
<td>0.126</td>
<td>BF_{10} = 0.739</td>
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<tr>
<td>l</td>
<td>Normally distributed</td>
<td>F test, main effect</td>
<td>&lt; 0.001</td>
<td>\eta^2 = 0.326</td>
</tr>
<tr>
<td>m1</td>
<td>Normally distributed</td>
<td>One-sided one sample t test</td>
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<td>BF_{10} = 0.254</td>
</tr>
<tr>
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<tr>
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<tr>
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<tr>
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<td>o</td>
<td>Normally distributed</td>
<td>F test, main effect</td>
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<td>BF₁₀ =</td>
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<td>p5</td>
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<td>0.841</td>
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<tr>
<td>q₁</td>
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<td>0.032</td>
<td>2.186</td>
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<tr>
<td>q₂</td>
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<td>3.841</td>
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<tr>
<td>r₁</td>
<td></td>
<td></td>
<td>&lt; 0.001</td>
<td>43.706</td>
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<tr>
<td>r₂</td>
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<td>0.003</td>
<td>13.818</td>
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<tr>
<td>r₃</td>
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<td>0.006</td>
<td>8.572</td>
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<tr>
<td>r₄</td>
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<td>0.007</td>
<td>7.511</td>
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<tr>
<td>r₅</td>
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<td>s₁</td>
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<td>F test, main effect</td>
<td>0.001</td>
<td>η² = 0.476</td>
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<td>s₃</td>
<td></td>
<td>F test, main effect</td>
<td>0.042</td>
<td>η² = 0.201</td>
</tr>
</tbody>
</table>

Disentangling location and temporal distance in adaptation in PHC

Evaluation of influences of passive movement phase on adaptation

Analysis of successful navigation effect
(a) Virtual environment and object layout

object layout in the nature environment

- 18m
- 4m
- 0m
- 2m
- 6m
- 10m
- 14m
- 22m

linear track

random start

arrows

Loc1

Loc2

Loc3

Loc4

landmark

nature environment

object layout in the city environment

- 18m
- 4m
- 0m
- 2m
- 6m
- 10m
- 14m
- 22m

linear track

random start

arrows

Loc1

Loc2

Loc3

Loc4

landmark

city environment

(b) Location identification task, trial time course

Landmark condition

1.2-16s

mean=5.2s

0.7s

1.5-2.5s

4s

mean=1.8s

Self-motion condition

(1) start

(2) movement

(3) location arrival

fMRI analysis

(4) location occupation

Pre-scan_day

Behavioral training

Outside scanner

MRI_day1

Scanning in 7T

8 fMRI runs

160 trials

MRI_day2

Scanning in 7T

8 fMRI runs

160 trials

(5) response

What is the ball color?

blue

yellow

red

purple

(6) feedback

correct

The ball is yellow

An example of Latin square counterbalancing

Run 1: landmark + nature

Run 2: landmark + city

Run 3: self-motion + city

Run 4: self-motion + nature

Run 5: self-motion + city

Run 6: landmark + nature

Run 7: self-motion + nature

Run 8: landmark + city
Behavioral accuracy: cue * location

Pre-scan_day

MRI_day1

MRI_day2

# correct / # total trials

Loc1 Loc2 Loc3 Loc4

Loc1 Loc2 Loc3 Loc4

Loc1 Loc2 Loc3 Loc4

- landmark
- self-motion
(a) Activation vs. distance

(b) Distance vs. location identity

(c) Neural space reconstruction analysis