Field Navigation Training Enhances Stability of Brain Functional Connectivity Patterns

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Abstract

Spatial navigation primarily relies on two spatial representations: egocentric reference representation and allocentric reference representation. However, how improvements in individuals' spatial navigation capabilities in real-world environments relate to these two representations remains unknown. To address this, the present study combined behavioral measurements with functional magnetic resonance imaging (fMRI) to analyze changes in spatial navigation ability and global functional connectivity patterns before and after real-world spatial navigation training in unfamiliar environments, systematically examining the underlying neural mechanisms of enhanced real-world spatial navigation ability. The results demonstrated that following training, participants in the training group exhibited significantly enhanced neural activity in the superior parietal lobule (SPL)—the core brain region for egocentric reference representation—when performing spatial navigation tasks. More importantly, training substantially increased the stability of the SPL-centered whole-brain functional connectivity pattern, which positively correlated with improvements in individual navigation task performance. These findings suggest that enhanced real-world spatial navigation ability is closely linked to strengthened egocentric representation, which further manifests as consolidated information exchange pathways between the SPL and other brain regions.

Full Text

Real-World Navigation Training Enhances the Stability of Brain Functional Connectivity Patterns

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Abstract

Spatial navigation relies primarily on two spatial representations: egocentric (body-centered) reference frames and allocentric (environment-centered) reference frames. However, the relationship between improvements in real-world navigation ability and these two spatial representations remains unclear. To address this question, the present study combined behavioral measurements with functional magnetic resonance imaging (fMRI) to analyze changes in spatial navigation ability and global brain functional connectivity patterns before and after real-world navigation training in an unfamiliar environment, systematically investigating the neural mechanisms underlying improvements in real-world navigation ability. The results revealed that after training, the training group showed significantly enhanced neural activity in the superior parietal lobule (SPL), a core brain region for egocentric reference representation, when performing spatial navigation tasks. More importantly, training significantly increased the stability of whole-brain functional connectivity patterns centered on the SPL, which positively correlated with improvements in individual navigation task performance.

These findings indicate that improvements in real-world navigation ability are closely associated with enhanced egocentric reference representation, which further manifests as the consolidation of information exchange pathways between the SPL and other brain regions.

Keywords: spatial navigation, egocentric reference, superior parietal lobule (SPL), functional connectivity pattern

Spatial navigation is a crucial ability in daily life. During navigation, people must familiarize themselves with various environmental information, such as the locations of landmarks and routes between buildings, process and integrate this information, and store it in memory, enabling rapid orientation and route finding when returning to the same environment (Epstein et al., 2017; Evans & Pezdek, 1980; Kitchin, 1994). Even with today's advanced electronic technology, we still rely on our navigation abilities to identify locations in many contexts, such as on campuses or between building floors. Faced with constantly changing spatial information during navigation, we depend on spatial reference frames that are both stable and flexible to encode and represent object locations. The brain represents object locations primarily based on two reference frames: egocentric reference (centered on the self or body) and allocentric reference (centered on the environment or other objects) (Klatzky, 1998; Montello, 1998; Vogeley & Fink, 2003). Egocentric reference representation involves spatial coding of objects through their relative positions to oneself. For example, "I am standing at the school gate, and the library is to my front-right."

Egocentric spatial representation also includes route information between landmarks, such as “go straight and then turn right” (Montello, 1998). Allocentric reference representation involves spatial coding of objects through their positional relationships with the environment or other objects, without involving one’s own position. Allocentric spatial representation typically includes the geometric structure between landmarks (such as a cognitive map). For instance, determining that “the library is north of the gymnasium” uses a polar coordinate system and represents an allocentric reference representation.

Numerous neuroscience studies have shown that egocentric and allocentric spatial representations involve distinct neural circuits that are anatomically and functionally separated (Byrne et al., 2007; Wolbers & Wiener, 2014). Allocentric representation primarily activates the medial temporal lobe, including the hippocampus, parahippocampus, and retrosplenial cortex (Jordan et al., 2004; Maguire et al., 1998; Morgan et al., 2011; Parslow et al., 2004; Rosenbaum et al., 2004; Spiers & Maguire, 2007; Suthana et al., 2009). In contrast, egocentric reference representation typically activates the frontoparietal network (Chen et al., 2012; Galati et al., 2000; Liu et al., 2017; Ruotolo et al., 2019; Saj et al., 2014), particularly the superior parietal lobule and precuneus in the posterior parietal cortex, which are frequently activated during egocentric navigation tasks (Parslow et al., 2004; Rosenbaum et al., 2004; Weniger et al., 2010).

Which spatial reference frame do individuals rely on more during real-world navigation? Previous research has preliminarily explored the use of these two spatial representation methods in navigation. First, Montello (1998) proposed that both egocentric and allocentric spatial information may begin to be acquired when we first encounter a new environment. Whether in a familiar or new environment, individuals can use either or both spatial representation methods to explore and navigate. Moreover, research has shown that individuals can skillfully switch between these two representation methods (Boccia et al., 2016; Taylor & Tversky, 1992). However, existing research suggests that individuals’ familiarity with an environment influences which spatial representation method is used, with cognitive map-like representations (i.e., allocentric reference representation) being more common for familiar environments (Siegel & White, 1975). The process of acquiring spatial knowledge in large-scale environments involves quantitative accumulation and refinement, where egocentric reference representation of landmarks and route information accumulates to a certain extent and is then organized within a unified reference frame to form a cognitive map (Montello, 1998). In other words, navigation in unfamiliar environments may rely more on egocentric reference representation.

To address these issues, previous studies have examined the neural mechanisms of navigation in both familiar and unfamiliar environments. Familiar environments are generally considered to be cities or areas where individuals have lived for many years and have rich navigation experience, accurately mastering the directions, routes, and distances between landmarks (Nemmi et al., 2013; Rosenbaum et al., 2007; Rosenbaum et al., 2004; Spiers & Maguire, 2007). Unfamiliar environments are those where individuals have had limited exposure or cannot navigate accurately. Studies of navigation in familiar environments have primarily used mental imagery tasks to examine the retrieval of spatial memories of familiar real-world environments (Nemmi et al., 2013; Rosenbaum et al., 2007; Rosenbaum et al., 2004; Spiers & Maguire, 2007). For example, one study found that adults with rich navigation experience in a city showed stronger activation in the posterior parietal cortex and retrosplenial cortex when performing mental imagery navigation tasks emphasizing egocentric reference representation (such as imagining the sequence of buildings when moving along a path) and allocentric reference representation (such as judging distances between buildings), respectively (Rosenbaum et al., 2004), suggesting that individuals possess both egocentric and allocentric representations for familiar environments, mediated by different brain regions. Studies of navigation in unfamiliar environments require navigation training methods to examine changes in navigation ability and the brain before and after learning in a novel environment. These studies have primarily used virtual environment videos or filmed real-world environment videos (Boccia et al., 2016; Iaria et al., 2007; Janzen et al., 2008; Janzen & Van Turennout, 2004) and real-world navigation learning (Schinazi & Epstein, 2010; Schinazi et al., 2013). For example, Schinazi et al. (2013) recruited adult participants for three simple real-world campus route learning sessions and found improved behavioral performance in direction estimation, distance estimation, and map drawing tests after learning. The angular error in offsite direction estimation tests negatively correlated with hippocampal volume. However, these real-world navigation training studies used simple route learning involving few landmarks and fixed paths that could be learned quickly, while virtual environment or video learning differs fundamentally from real environments in complexity and flexibility. Therefore, existing research cannot reveal the cognitive and neural mechanisms underlying gradual improvements in navigation ability in unfamiliar, complex real-world environments, nor can it determine which spatial representation method real-world navigation ability improvement relies on more.

Consequently, the present study employed a complex real-world spatial navigation training method to investigate which spatial reference frame individuals primarily rely on when improving their spatial navigation ability in unfamiliar real-world environments and the underlying neural mechanisms. To this end, we recruited university freshmen as participants and conducted a 20-day campus real-world navigation training program. Before and after training, participants completed a series of behavioral tests assessing spatial orientation, distance, and route judgment (Schinazi et al., 2013) and functional magnetic resonance imaging (fMRI) experiments (Hirshhorn et al., 2012; Rosenbaum et al., 2004), which were compared with a control group that received no navigation training to examine changes in behavior and neural activity before and after training. Previous research has shown that using absolute coordinates (e.g., facing north) leads to better orientation perception in familiar environments and better learning of new environments (Frankenstein et al., 2012; Gagnon et al., 2014). Moreover, the degree of absolute coordinate system use positively correlates with individuals' direction perception ability in real environments and with gray matter volume in the entorhinal cortex, where grid cells are located (Hao et al., 2017). Therefore, this study used the cardinal directions (north, south, east, west) coordinate system for route guidance training to examine the involvement of egocentric and allocentric reference representation systems in real-world navigation in unfamiliar environments. We hypothesized that: (1) short-term absolute coordinate guidance training might cause a shift from egocentric to allocentric reference representation systems, with brain regions related to allocentric representation becoming more involved in navigation after training (i.e., navigation method dominates brain navigation system use); or (2) in unfamiliar environments, even as the environment becomes more familiar, the egocentric reference representation system continues to participate in navigation and becomes more efficient (i.e., environment dominates brain navigation system use).

It is worth noting that previous navigation training studies have primarily focused on regional brain changes (Boccia et al., 2014; Byrne et al., 2007; Kravitz et al., 2011; Spiers & Maguire, 2006), examining only training-induced changes in local regional activation or inter-regional functional connectivity (Boccia et al., 2016; Schinazi & Epstein, 2010). In recent years, many learning studies have found that various types of learning induce global brain changes (Bassett et al., 2011; Bassett et al., 2015; Mohr et al., 2016), particularly increased stability of large-scale functional connectivity patterns (FC pattern) (Yu et al., 2020) or increased similarity to target states (Dresler et al., 2017; Yu et al., 2021). Therefore, this study further investigated the global brain changes induced by real-world spatial navigation learning.

Previous behavioral and fMRI studies on spatial navigation training have used sample sizes of approximately 14 to 16 participants to obtain significant training effects (Boccia et al., 2016; Boccia et al., 2014; Schinazi & Epstein, 2010; Schinazi et al., 2013). Therefore, this study recruited 32 university students (19 females, 13 males) from a university in Beijing, aged 19-24 (M = 20.23, SD = 1.68), who were randomly divided into a training group (n = 16, 9 females, 7 males) and a control group (n = 16, 10 females, 6 males). All participants were first-year freshmen, and the experiment was conducted three months after their enrollment. All participants had normal or corrected-to-normal vision and no history of cognitive disorders, mental illness, or brain injury before participating in the experiment. None of the participants had a habit of using cardinal directions for orientation or route guidance before the experiment. This study was approved by the Ethics Committee of Beijing Normal University. All participants signed informed consent forms and received appropriate compensation after the experiment.

Experimental Procedure

The entire experiment consisted of three phases: a training phase and pre-training and post-training testing phases (hereinafter referred to as "pre-test" and "post-test"). The training phase lasted 20 days, during which training group participants received real-world navigation training on campus, while control group participants received no training. During the pre-test and post-test phases, both groups completed a series of navigation ability-related behavioral tests and fMRI experiments. The behavioral tests and fMRI experiments in the pre-test phase were completed within two days before training began; the post-test phase involved the same behavioral tests and fMRI experiments as the pre-test phase, completed within two days after training ended. Specific details of the navigation training process, fMRI experiments and data analysis, and navigation ability behavioral tests are described in sections 2.3 to 2.5 below.

Spatial Navigation Training

Training group participants underwent 20 days of real-world spatial navigation training, averaging 30 minutes per day, with the task of using cardinal directions to complete route guidance tasks assigned by the experimenter in real-time. This study used the cardinal directions coordinate system rather than left/right for route guidance training for two reasons: (1) previous research has shown that using absolute coordinates leads to better orientation perception in familiar environments and better learning of new environments (Frankenstein et al., 2012; Gagnon et al., 2014); (2) using the cardinal directions coordinate system facilitates judging whether participants' route guidance was correct during training, improving the operability of the training process. The landmark locations used in training were 50 relatively dispersed locations on campus selected through a pilot experiment, including familiar locations such as the library and main teaching buildings, as well as unfamiliar locations such as laboratory buildings and affiliated primary schools, as shown in [Figure 1: see original paper]. During training, participants arrived at one of these 50 locations (starting position) and sent their real-time location to the experimenter via WeChat. The experimenter immediately randomly designated another location as the destination and required participants to verbally describe, within one minute using cardinal directions, the shortest walking route from the starting position to the destination as quickly, accurately, and specifically as possible. After completing their response, the experimenter provided feedback. If the participant's response was incorrect, the experimenter would inform them of the shortest route and require them to walk from their current location to the destination to learn it; if the response was correct, they did not need to walk to the destination and could directly begin the next route guidance task. During each day's training, participants needed to be at least 3 different locations on campus (starting positions) to complete 12-15 route guidance tasks, with the starting position changing every 3-5 tasks. Over the 20 days of training, the 50 designated locations appeared as destinations for a total of 5 rounds, comprising 250 route guidance tasks. We calculated the accuracy rate for each round as a behavioral performance indicator during training. To ensure effective training, all participants had lived on campus for 3 months and were already familiar with most major landmark buildings before the experiment (see pre-test landmark familiarity self-rating results). Additionally, the route guidance task questions did not overlap with any questions in the pre-test or post-test.

fMRI Experiment and Data Analysis

Experimental Design

During the pre-test and post-test phases, participants underwent one MRI scan each, with each scan including structural imaging and task-based imaging. The task-based imaging included two experimental tasks: a distance judgment task (Hirshhorn et al., 2012; Rosenbaum et al., 2004) and a paper folding task (Milivojevic et al., 2003; Shepard & Feng, 1972). The former was a spatial navigation training-related test task, while the latter served as a control task.

The distance judgment task required participants to determine which of two locations appearing on the screen was closer to a "target location" in terms of shortest path distance ([Figure 2: see original paper]A). The same "target location" was used throughout the experiment, which participants were informed about via instructions, and the experimenter confirmed that participants were familiar with this location. This "target location" was situated at the center of campus (see star location in [Figure 1: see original paper]) and was highly familiar to participants. This task did not restrict which spatial reference strategy to use; participants could employ either egocentric reference (imagining themselves standing at the target location and judging the walking distance of the other two locations from themselves) or allocentric reference (judging the path distance between the two locations and the target location in a cognitive map). The experiment used a block design with 4 runs, each including 6 experimental task blocks and 7 fixation blocks, alternating between them. Each experimental task block included 4 trials, with each trial lasting 8 seconds. In each trial, two location names appeared on the left and right sides of the screen, and participants were required to accurately judge which location was closer to the "target location" and respond with the corresponding button. The location names disappeared after 6 seconds, followed by a 2-second blank screen, and participants could respond within the 8-second period after the location names first appeared. Fixation blocks lasted 12 seconds, during which participants did not need to make any response.

In the paper folding task, a flat 2D net of a cube was presented in the center of the screen ([Figure 2: see original paper]B), with the dark square representing the bottom face of the cube. Participants were required to accurately judge whether the two edges indicated by arrows on the net would coincide when folded into a cube and respond with a button press. This task also used a block design with 4 runs, and the experimental design was consistent with the distance judgment task. In each trial, the net was presented for 6 seconds, followed by a 2-second blank screen, and participants needed to make a button response within 8 seconds after the image first appeared.

Data Acquisition

Data were collected using a Siemens 3.0 T MRI scanner. Functional imaging used an echo-planar imaging (EPI) sequence with the following parameters: TR = 2000 ms, TE = 30 ms, flip angle FA = 90°, voxel size = 3.125 mm × 3.125 mm × 3.5 mm, FOV = 200 mm × 200 mm, number of slices = 33. T1-weighted structural images were acquired using a magnetization-prepared rapid gradient echo (MP-RAGE) sequence with parameters: TR/TE/TI = 2530/3.39/1100 ms, flip angle FA = 7°, voxel size = 1 mm × 1 mm × 1.33 mm. Participants wore earplugs to reduce scanner noise interference. To prevent head movement, sponge pads were placed between the head coil and participants' heads.

Data Quality Control

Data quality control was based on two main indicators: first, participants' head movement during scanning, for which we excluded runs with maximum translation exceeding 2 mm or maximum rotation exceeding 2°; second, participants' task performance, for which we excluded runs with three or more consecutive trials without button responses. The data situation was as follows: In the distance judgment task, 2 runs were excluded due to excessive head movement (from two participants), and another 2 runs were excluded due to low task completion quality (from two participants). In the paper folding task, 4 runs were excluded due to excessive head movement, with 3 runs from one training group participant's pre-test scan, resulting in exclusion of that participant's data; another run was excluded due to low task completion quality. Therefore, the distance judgment task retained data from 32 participants, while the paper folding task retained data from 31 participants.

fMRI Data Analysis

Activation Analysis. We used the FEAT tool in FSL software (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/) to analyze the functional imaging data from the two fMRI experimental tasks before and after training. First, we performed "first-level analysis" for each run of each participant's pre-test and post-test scans. Image preprocessing steps included: motion correction, spatial smoothing (full width at half maximum of 5 mm), intensity normalization, and high-pass filtering (0.01 Hz). Next, we used the FILM (FMRIB's Improved Linear Model) tool for statistical analysis of time series. In the general linear model, task conditions were set as explanatory variables (EVs), modeling the onset time and duration of stimulus presentation and convolving them with the hemodynamic response function (HRF). Six motion parameters extracted during motion correction were included in the model as confounding factors. Statistical Contrasts were used to estimate signals for task conditions.

After the "first-level analysis," we performed "higher-level analysis" for all runs of each participant's each scan. First, we used FSL's linear registration tool FLIRT to align the statistical parametric images obtained from the "first-level analysis” to each participant’s structural image, and then used the nonlinear registration tool FNIRT to register the aligned images to the standard MNI template (2 mm × 2 mm × 2 mm). Then, we used fixed-effect analysis to integrate and analyze the spatially normalized images from multiple runs, and performed statistical contrasts for the two groups’ pre-test and post-test scans, namely “post-test > pre-test.” Finally, we used mixed-effect analysis to statistically compare the differences between the two groups’ pre-test and post-test scans, namely “training group pre-post difference > control group pre-post difference.”

Functional Connectivity Pattern Similarity Analysis. Methods for calculating the spatial distribution patterns of functional connectivity can characterize process-related or state-related large-scale brain region information interactions during resting or task states (Dresler et al., 2017; Keerativittayayut et al., 2018; Tambini et al., 2017), and can be used to examine similarities or stability of brain global connectivity patterns across participants, conditions, and time. This study investigated whether navigation training improved the stability of information interaction between core brain regions and the whole brain during task states, and whether this was specific to navigation-related memory retrieval processes.

Before calculating functional connectivity, we re-preprocessed the raw data to obtain relatively pure background signals for calculating background functional connectivity (background FC) during task states (Tambini et al., 2017). Preprocessing steps included: motion correction, spatial smoothing (full width at half maximum of 5 mm), intensity normalization, removal of physiological noise and task effects, and elimination of low-frequency drift and high-frequency noise through band-pass filtering (0.01~0.1 Hz). To eliminate physiological noise from head movement, heartbeat, and respiration, and to remove task effects to obtain pure background functional connectivity, we used a “regression method” to control for the following variables: average cerebrospinal fluid signal, white matter signal, six motion parameters from motion correction and their derivatives, and task effects. Finally, the 4D residual time series images with these confounding variables removed were registered to MNI standard space.

The processed 4D data were used to calculate background functional connectivity during task states. First, the time series of task blocks were normalized block-wise and concatenated to form the time series for each run under task state. Then, based on the results from the activation analysis above, seed regions were selected, and seed-based functional connectivity (seed-based FC) was calculated for each run of each participant’s each scan across the whole brain. Specifically, for each run, the average time series of all voxels within the seed region was extracted, and Pearson correlation coefficients were calculated with the time series of each voxel in the whole brain gray matter template. The correlation coefficient r values were converted to Z values through Fisher’s Z transformation to obtain functional connectivity Z-value maps. [Figure 6: see original paper]A presents the functional connectivity Z-value maps from 4 runs in the pre-test distance judgment task scan for one participant, with the right superior parietal lobule (rSPL) as the seed point.

Finally, we analyzed the stability of functional connectivity patterns. We calculated the pattern similarity between functional connectivity maps for each run in each participant's pre-test and post-test scans. Specifically, for the functional connectivity maps from 4 runs of the distance judgment task in pre-test or post-test scans, we used Pearson correlation to calculate the spatial similarity r values between each pair and then calculated their average as an indicator of connectivity pattern stability for that task (as shown in [Figure 6: see original paper]A). The same method was used to calculate connectivity pattern stability for each participant in the pre-test and post-test paper folding tasks as a control task stability indicator.

Navigation Ability Behavioral Tests

Based on previous research, familiarity with the overall environment includes not only familiarity with landmarks but also accurate knowledge of spatial information such as directions, routes, and distances between landmarks. To comprehensively measure participants' familiarity with the campus environment and navigation ability before and after training, we conducted a series of behavioral tests related to direction, distance, and route information during the pre-test and post-test phases (Nori & Piccardi, 2011; Schinazi et al., 2013), including live pointing tests, offsite direction estimation, straight-line distance estimation, and route distance estimation tasks. Additionally, participants completed a self-rating of landmark familiarity.

The purpose of the landmark familiarity self-rating was to investigate participants' familiarity with various landmark buildings on campus that would be used in testing and training, to ensure the effectiveness of navigation training and direction, route, and distance tests (i.e., participants knew which landmark was being referred to), and to control for the absence of significant differences in landmark familiarity between the two groups before the experiment. This self-rating questionnaire consisted of 50 items, each corresponding to one location, requiring participants to rate "whether they know and are familiar with this location on campus and its approximate location" on a 1-7 scale, where 1 indicated very unfamiliar and 7 indicated very familiar. Pre-test results showed that both groups were basically familiar with the 50 landmarks that would be used in the experiment (training group $M = 5.35$, $SD = 0.97$; control group $M = 5.12$, $SD = 0.81$; $t(30) = 0.70$, $p = 0.487$), ensuring the effectiveness of direction, route, and distance tests and navigation training.

The live pointing test was conducted in a behavioral laboratory near the center of campus. A circular angle disk marked with 0° to 360° was placed on the laboratory floor, with 0° representing true north. Participants stood at the center of the angle disk facing the 0° direction and pointed on the angle disk to indicate the direction of target locations given by the experimenter relative to their current position. Before testing, participants confirmed their location and orientation. The laboratory contained no other location reference information (such as windows). This test consisted of 44 trials, each corresponding to one target location, which were obtained by removing locations less than 30 meters from the laboratory from the 50 designated locations. We calculated the error between participants' estimated direction angle and the actual angle for each trial as an indicator of live direction estimation accuracy bias. Smaller angular error indicated higher direction estimation accuracy.

The offsite direction estimation test was a paper-and-pencil test consisting of 20 items, each comprising two locations (e.g., Location A and Location B), requiring participants to imagine standing at Location A facing true north (0°) and indicate the direction of Location B relative to Location A. An example item with the answer was provided before testing as a reference. For each item, we calculated the error between participants' estimated angle and the actual angle as an indicator of offsite direction estimation accuracy bias.

The distance estimation test included two subtests: shortest route distance estimation and straight-line distance estimation. This test was also a paper-and-pencil test, with each subtest containing 20 items, each comprising two locations, requiring participants to estimate the shortest route distance or straight-line distance between the two locations in meters. An example item with the answer was provided before testing as a reference. For each item, we calculated the error between participants' estimated distance and the actual distance, and calculated the average error for each subtest as an indicator of straight-line distance and route distance estimation accuracy bias. Smaller distance error indicated higher accuracy.

Training group participants underwent continuous real-world navigation training for 20 days. Throughout the training process, the 50 locations were randomly designated as route guidance targets for a total of 5 rounds. We calculated the average accuracy rate for each round of 50 route guidance tasks as participants' behavioral performance indicator during training (as shown in [Figure 3: see original paper]).

ANOVA results showed that participants' route guidance accuracy rates improved significantly during training, $F(4, 60) = 33.26$, $p < 0.001$, $^{2} = 0.69$. Results from pairwise one-tailed paired t-tests showed that the average accuracy rate increased significantly between the first and second rounds ($t(15) = 5.26$, $p < 0.001$, Cohen's $d = 1.32$; Bonferroni corrected), and continued to show a gradual improvement trend thereafter ($ts > 1.47$, $ps < 0.081$, Cohen's $ds > 0.36$). These results indicate that participants gradually became familiar with and mastered the directions and routes between various locations during real-world navigation training, gradually forming a cognitive map of the campus.

fMRI Experimental Behavioral Results

To examine training effects, we used one-tailed paired samples t-tests to compare pre-test and post-test behavioral data for the training and control groups separately, and two-tailed independent samples t-tests to analyze between-group differences in pre-post changes (post-test minus pre-test). In the distance judgment task, participants' behavioral performance was analyzed in terms of accuracy, reaction time, and response efficiency, with descriptive statistics shown in . First, accuracy analysis revealed that both groups' average accuracy rates in pre-test and post-test were significantly higher than chance level of 50% (one-tailed one-sample t-tests, ts > 12.95, ps < 0.001, Cohen's ds > 3.32), indicating that participants completed the experimental tasks seriously and effectively. Next, we examined training effects. Considering the high difficulty of this experimental task and the long reaction times (M = 4.35 s, SD = 0.8), participants might use different response strategies involving trade-offs between reaction time and accuracy. Therefore, we adopted a response efficiency index (accuracy/reaction time) (Jonker et al., 2013; Reifegerste et al., 2020).

Results showed that the training group's response efficiency in the post-test distance judgment task was significantly higher than in the pre-test ($t(15) = 5.93$, $p < 0.001$, Cohen's $d = 1.48$), while the control group showed no significant difference between pre-test and post-test ($t(15) = 0.16$, $p = 0.436$). Moreover, the change in response efficiency between pre-test and post-test differed significantly between the training and control groups ($t(30) = 3.48$, $p = 0.002$, Cohen's $d = 1.23$; [Figure 4: see original paper]A). These results further demonstrate that real-world navigation training improved the accuracy of participants' spatial distance representation information, which could be effectively retrieved during the distance judgment task state.

Participants' behavioral performance in the paper folding task was also analyzed in terms of accuracy, reaction time, and response efficiency, with descriptive statistics shown in . First, we examined the validity of this task. One-tailed one-sample t-test results showed that both groups' average accuracy rates in pre-test and post-test were significantly higher than chance level of 50% (ts $>$ 9.17, ps < 0.001, Cohen's ds > 2.30), indicating that participants completed the experimental task seriously and effectively. Next, we examined whether training effects existed in the paper folding task. We also used the response efficiency index (accuracy/reaction time). Statistical analysis of pre-post differences in response efficiency showed that both the training and control groups had significantly higher response efficiency in post-test than in pre-test (training group: $t(15) = 4.07$, $p = 0.001$, Cohen's $d = 1.02$; control group: $t(15) = 2.37$, $p = 0.016$, Cohen's $d = 0.59$). However, the change in response efficiency between pre-test and post-test did not differ significantly between the two groups ($t(30) = 0.60$, $p = 0.551$; [Figure 4: see original paper]B), indicating that the training group's improved response efficiency in post-test paper folding judgment was due to practice effects rather than training results, and also showing that the effects of large-scale spatial navigation training did not transfer to this small-scale spatial imagination task.

fMRI Data Results

Training Effects on Activation

First, we examined activation differences in the training group between pre-test and post-test in the distance judgment task (post-test > pre-test) and found significantly stronger activation after training in multiple regions, including the intraparietal sulcus, cingulate and paracingulate gyri, superior frontal gyrus, frontal pole, precuneus, and caudate nucleus, as shown in . The control group showed no significantly different activation regions between pre-test and post-test in the distance judgment task.

Next, we further examined training-induced changes in activation intensity in the distance judgment task by testing brain regions showing "training group pre-post difference > control group pre-post difference." Results revealed a significant activation intensity difference in a cluster in the posterior ventral part of the right parietal lobe, located in the superior parietal lobule (SPL) extending to the precuneus (125 voxels, MNI peak coordinates: 20, -66, 58; [Figure 5: see original paper]A). This result indicates that real-world navigation training induced activation changes in the rSPL region during distance judgment, suggesting that this region is a core brain area related to improved real-world navigation ability after training. The SPL is a core brain region for egocentric reference spatial representation, so this result also suggests that improvement in real-world navigation ability primarily relies on egocentric reference representation, and that during the distance judgment task, participants mainly relied on egocentric reference representation information for rapid estimation and comparison of path distances between locations.

Functional Connectivity Pattern Analysis Results

Next, we further examined whether real-world navigation training induced global brain activity pattern changes and tested whether improvement in real-world navigation ability was related to increased stability of connectivity patterns between the core brain region of self-referential navigation learning (rSPL) and the whole brain. By calculating background functional connectivity during the distance judgment task and comparing pre-post changes in connectivity pattern stability between rSPL and whole-brain voxels, we found that the training group's connectivity pattern stability in the post-test distance judgment task was significantly higher than in the pre-test ($t(15) = 3.17$, $p = 0.003$, Cohen's $d = 0.79$), while the control group showed no significant difference between pre-test and post-test ($t(15) = 0.42$, $p = 0.342$). Moreover, the change in connectivity pattern stability between pre-test and post-test differed significantly between the training and control groups ($t(30) = 2.62$, $p = 0.014$, Cohen's $d = 0.93$; [Figure 6: see original paper]B). These results indicate that the training group's increased connectivity pattern stability after training was mainly caused by navigation training rather than practice effects from the two test sessions. These findings suggest that real-world navigation training improved the stability of connectivity patterns between the right SPL and whole-brain voxels during distance judgment, indicating that training consolidated the information exchange pathways between the SPL and other brain regions, enabling participants to extract direction and route information more stably and efficiently for distance judgment.

Furthermore, we examined whether the increased connectivity pattern stability found in the above analysis was specific to training-related tasks or cognitive processes, namely the distance judgment process. Therefore, we used the same method to test changes in functional connectivity pattern stability in the control task. Results showed that the training group's connectivity pattern stability in the pre-test and post-test paper folding tasks did not differ significantly (t(14) = 0.33, p = 0.374), and the control group also showed no significant difference between pre-test and post-test (t(15) = 1.06, p = 0.152). The change in connectivity pattern stability between pre-test and post-test also did not differ significantly between the two groups (t(29) = 0.95, p = 0.351; [Figure 6: see original paper]C). Additionally, the interaction effect of connectivity pattern stability changes between the two groups in the distance judgment and paper folding tasks was significant, F(1, 29) = 12.76, p = 0.001, ^{2} = 0.31. These results indicate that the increased connectivity pattern stability induced by navigation training was specific to the training-related spatial distance judgment process.

Finally, we examined the behavioral significance of the increased functional connectivity pattern stability induced by navigation training and tested its correlation with behavioral performance in the distance judgment task. We calculated the change in background connectivity pattern stability between rSPL and whole-brain voxels in the distance judgment task for each training group participant (post-test minus pre-test) and calculated its correlation with the change in response efficiency in that task (post-test minus pre-test). Results showed that the change in whole-brain connectivity pattern stability between pre-test and post-test was significantly positively correlated with the change in distance judgment behavioral performance across participants (Pearson correlation r = 0.55, p = 0.028; Spearman correlation r = 0.50, p = 0.048; [Figure 7: see original paper]). These results indicate that after real-world navigation training, the greater the improvement in participants' behavioral performance in the distance judgment task, the greater the increase in connectivity pattern stability between the egocentric reference representation core brain region SPL and the whole brain, suggesting that increased stability of connectivity patterns between the SPL and various brain regions may be the neural mechanism underlying more efficient distance judgment. Additionally, we conducted a correlation analysis between changes in SPL activation intensity and distance judgment behavioral performance in the training group, which showed no significant correlation (Pearson correlation r = 0.02, p = 0.935). This result suggests that improved distance judgment performance after training may depend more on the stability of connectivity pathways between the SPL and whole brain rather than activation intensity in a single brain region.

Navigation Ability Behavioral Test Results

To more comprehensively measure changes in participants' familiarity with the campus environment and navigation ability before and after training, this study also conducted a series of behavioral tests including live pointing, offsite direction estimation, straight-line distance estimation, and route distance estimation to measure the accuracy of participants' spatial representation information about the campus from three aspects: direction, distance, and route between landmarks. Among these, offsite direction estimation primarily measures allocentric representation spatial information, while other tests can use information from both representation types (Schinazi et al., 2013). For data from each behavioral test, we first used two-tailed independent samples t-tests to examine whether there were differences between the two groups' performance in the pre-test phase, then used one-tailed paired samples t-tests to compare pre-test and post-test behavioral data for the training and control groups separately, and used two-tailed independent samples t-tests to analyze between-group differences in pre-post changes (post-test minus pre-test).

For landmark familiarity self-rating, we first compared the two groups' self-rated familiarity with campus locations in the pre-test phase, finding no significant difference ($t(30) = 0.70$, $p = 0.487$). Next, analysis of pre-post differences revealed that the training group's familiarity with locations improved significantly after training (post-test $M = 6.24$, $SD = 0.88$; $t(15) = 4.98$, $p < 0.001$, Cohen's $d = 1.24$), while the control group showed no significant difference between pre-test and post-test (post-test $M = 5.29$, $SD = 0.93$; $t(15) = 1.05$, $p = 0.156$). Moreover, the change in familiarity between pre-test and post-test differed significantly between the two groups ($t(30) = 3.10$, $p = 0.004$, Cohen's $d = 1.09$).

For the live pointing task, there was no significant difference in pointing angle error between the two groups in the pre-test phase ($t(30) = 1.04$, $p = 0.306$). Analysis of pre-post changes showed that the training group's pointing error decreased significantly ($t(15) = 2.88$, $p = 0.006$, Cohen's $d = 0.72$), while the control group's performance did not differ significantly between pre-test and post-test ($t(15) = 1.56$, $p = 0.069$). Additionally, the change in pointing error between pre-test and post-test differed significantly between the two groups ($t(30) = 2.14$, $p = 0.041$, Cohen's $d = 0.76$; [Figure 8: see original paper]A), indicating that the training group's improved post-test performance was not due to practice effects from repeated testing but was caused by training. These results demonstrate that real-world navigation training improved participants' accuracy in representing directional relationships between campus locations in live testing.

For the offsite direction estimation test, there was no significant difference in direction estimation angle error between the two groups in the pre-test phase ($t(30) = 0.40$, $p = 0.693$). Analysis of pre-post changes showed no significant difference in direction estimation error between pre-test and post-test for either the training group (t(15) = 1.34, p = 0.10) or the control group (t(15) = 0.37, p = 0.360), and the change in direction estimation error between pre-test and post-test did not differ significantly between the two groups (t(30) = 0.59, p = 0.559; [Figure 8: see original paper]B). This result indicates that real-world navigation training did not significantly improve participants' offsite direction estimation ability.

The distance estimation test included two subtests: shortest route distance estimation and straight-line distance estimation. For shortest route distance estimation, there was no significant difference in estimation error between the two groups in the pre-test phase (t(30) = 0.31, p = 0.757). Analysis of training effects revealed that the training group's post-test estimation error was significantly smaller than pre-test (t(15) = 2.00, p = 0.032, Cohen's d = 0.50; [Figure 8: see original paper]C), while the control group's performance did not differ significantly between pre-test and post-test (t(15) = 0.07, p = 0.471). The difference in estimation error change between pre-test and post-test between the two groups did not reach significance[1] (Mann-Whitney U test Z = 1.66, p = 0.097). For straight-line distance estimation, there was no significant difference in estimation error between the two groups in the pre-test phase (t(30) = 0.33, p = 0.741). Analysis of training effects showed that the training group's distance estimation error after navigation training was significantly smaller than before training (t(15) = 2.61, p = 0.010, Cohen's d = 0.65; [Figure 8: see original paper]D), while the control group showed no significant difference between pre-test and post-test (t(15) = 0.11, p = 0.456), and the change in straight-line distance estimation error between pre-test and post-test differed significantly between the two groups (t(30) = 2.18, p = 0.037, Cohen's d = 0.77). These results indicate that navigation training significantly improved participants' accuracy in estimating routes and distances between landmarks on campus.

Overall, participants showed large errors in estimating directions, route distances, and straight-line distances between landmarks in the pre-test, indicating unfamiliarity with the overall environment involved in the experiment. After 20 days of training, the training group showed significantly improved accuracy in mastering directions, routes, and distances between landmarks.

Discussion

This study used a real-world navigation training method to examine the cognitive and neural mechanisms underlying improvements in real-world navigation ability from behavioral, brain activation, and functional connectivity perspectives. Behaviorally, we found that navigation training improved participants' accuracy in live pointing, distance estimation, and distance judgment. At the neural level, compared with the control group, the training group showed significant differences in rSPL activation between pre-test and post-test in the distance judgment task. More importantly, during distance judgment, the training group showed significantly increased stability of functional connectivity patterns between rSPL and whole-brain voxels after training, which was significantly positively correlated with participants' behavioral performance in this task.

These findings indicate that improvement in real-world navigation ability in an unfamiliar environment primarily relies on enhanced egocentric spatial representation, and that navigation training may consolidate information exchange pathways between the egocentric reference representation core brain region SPL and other brain regions, thereby making spatial information retrieval more efficient.

This study found changes in SPL activation rather than medial temporal lobe regions in the distance judgment task before and after real-world navigation training. Previous research has consistently shown that the SPL is a core brain region for egocentric reference spatial representation. Early studies of brain-damaged patients found that patients with SPL damage had egocentric reference orientation deficits—they could not judge the positional relationships between objects or landmarks relative to themselves, often performing poorly in wayfinding tasks, though their ability to recognize objects and landmarks in the environment was not affected (Aguirre & D'Esposito, 1999). Subsequent studies also found that patients with posterior parietal cortex (PPC) damage performed poorly in a series of spatial tasks that primarily used egocentric reference strategies, such as mental imagery navigation (Ciaramelli et al., 2010) and virtual maze tasks (Weniger et al., 2009). Neuroimaging studies have also consistently found SPL activation during egocentric navigation tasks (Parslow et al., 2004; Rosenbaum et al., 2004; Weniger et al., 2010), three-dimensional scene transformation judgment tasks (Sulpizio et al., 2013), and object orientation judgment tasks (Chen et al., 2012; Galati et al., 2000; Liu et al., 2017; Neggers et al., 2006; Ruotolo et al., 2019). Moreover, scenes with better memory effects in real-world navigation learning (such as turning points) activated bilateral SPL more than scenes without special memory significance during recognition (Schinazi & Epstein, 2010), indicating that SPL activation is related to memory effects for building locations or scenes in real-world navigation. Additionally, as mentioned earlier, the distance judgment task in this study did not restrict the use of egocentric or allocentric strategies. Therefore, changes in SPL activation intensity before and after navigation training can be considered as indicating that participants primarily relied on egocentric reference representation information for path distance comparison between landmarks after training, suggesting that spatial location coding primarily depended on the egocentric reference system during real-world navigation learning.

Further functional connectivity multivariate pattern analysis results found that, compared with the control group, the training group's stability of functional connectivity patterns between rSPL and whole-brain voxels during distance judgment increased significantly after training and was positively correlated with distance judgment behavioral performance. This result suggests that increased stability of large-scale functional connectivity patterns in the core brain region for egocentric reference representation (rSPL) may be the mechanism underlying improved real-world navigation ability. Previous research has shown that neural pattern stability plays an important role in learning, including stability of activation patterns in specific brain regions (Bi et al., 2014; Huang et al., 2013; Visser et al., 2011) and stability of large-scale functional connectivity patterns (Yu et al., 2020). Specifically, at the brain region activation level, a series of studies have shown that more stable activation patterns in brain regions related to learning content are associated with stronger face discrimination ability (Bi et al., 2014), better memory encoding (Xue et al., 2010), and more skilled sequential motor movements (Huang et al., 2013), and are not affected by activation intensity (Xue et al., 2010). Researchers believe that learning reduces internal noise in neuronal responses to trained stimuli, making responses more consistent and representations more stable (Dosher & Lu, 1998). At the functional connectivity level, studies have found that finger sequence motor learning increased the stability of functional connectivity patterns between the primary motor cortex corresponding to the trained hand and whole-brain voxels, which was significantly positively correlated with behavioral performance improvement (Yu et al., 2020). These findings suggest that neural pattern stability may be a universal neural marker of effective learning.

Furthermore, unlike face perception learning (Bi et al., 2014) or sequential motor learning (Huang et al., 2013; Yu et al., 2020) involving stimulus or item repetition, the training and experimental tasks in this study did not involve repeated stimuli—each trial used a different combination of location names. Therefore, this study's results demonstrate that learning-induced increases in large-scale functional connectivity pattern stability are process-specific rather than stimulus- or item-specific. Functional connectivity pattern stability differs from regional activation pattern stability mentioned above—it does not reflect stimulus representation stability but rather reflects the stability and efficiency of information exchange pathways between large-scale brain networks during learning content retrieval. Specifically, learning may enhance effective connectivity pathways between core brain regions and other brain regions while weakening ineffective pathways, thereby optimizing information exchange pathways that gradually become consolidated during learning, making information retrieval faster and more accurate after learning. Moreover, related research has found that learning increases the similarity between large-scale brain network functional connectivity patterns and target states or target objects' functional connectivity patterns, gradually approaching a more effective connectivity pattern (Dresler et al., 2017; Yu et al., 2021). For example, one study found that after six weeks of memory strategy training, ordinary participants showed significantly improved memory ability, and the functional connectivity patterns between nodes in brain networks related to visuospatial processing and memory became more similar to those of world memory champions (Dresler et al., 2017). Combined with these studies, we propose that the learning process gradually stabilizes and consolidates functional connectivity patterns between brain regions toward an efficient target state, thereby achieving learning effects. Therefore, this study's results suggest that real-world navigation learning consolidates the interaction pathways between rSPL and various brain regions, making spatial information retrieval faster and more accurate after learning.

Additionally, to more comprehensively measure participants' navigation ability in the campus environment, this study conducted a series of behavioral tests related to direction, distance, and route. Compared with the control group, the navigation training group showed significantly improved behavioral performance in post-test live pointing, offsite route and distance tests, which corresponded with their steadily improving accuracy in completing route guidance tasks during training. However, the training group did not show significant improvement in post-test offsite direction estimation performance. Previous research suggests that offsite direction estimation primarily measures allocentric spatial representation, while other tests may include both types of representation (Schinazi et al., 2013). This result suggests that the real-world navigation training conducted in an unfamiliar complex environment in this study may not have achieved obvious improvement effects on spatial tasks that primarily rely on allocentric representation, at least not within the training period. However, it should be noted that these behavioral test results cannot provide direct evidence for the relationship between improved navigation ability induced by real-world navigation training and egocentric reference representation.

Finally, it is worth noting that which spatial reference frame individuals use more or enhance in spatial navigation may be influenced by multiple factors including environmental familiarity, coordinate system used, and navigation learning method. On one hand, from the perspective of coordinate systems used, the relative direction coordinate system of left/right is often considered an egocentric reference frame, while the cardinal directions coordinate system is considered an allocentric reference frame. On the other hand, previous navigation research often considers immersive real-world exploration or route learning as egocentric reference representation spatial navigation learning, while viewing map-based navigation learning as allocentric reference representation navigation learning (Boccia et al., 2016). However, this study's results found that even when using the cardinal directions absolute coordinate system for navigation training, individuals still primarily relied on the egocentric reference representation system for spatial information coding when navigating in unfamiliar real-world environments—that is, the environment dominates brain navigation system use.

This study has several limitations. First, this study only collected measurement data at two time points before and after training, providing a relatively coarse depiction of the learning process of behavioral performance and brain activity changes. Future research could examine brain functional network organization patterns before learning, during learning, immediately after learning, and after a period following learning to characterize more comprehensive global brain changes induced by learning. Second, although this study controlled for possible confounding variables while attempting to restore real-world complex navigation contexts, because the training environment was participants' real living environment, we could not exclude the possibility that participants might reinforce their familiarity with the environment in daily life, nor could we avoid potential individual differences in familiarity changes resulting from this. Additionally, participants' pre-existing familiarity with training locations before the experiment might also have affected the results. Future research could consider using environments completely unfamiliar to participants for navigation learning. Third, although this study found correlations between training-induced connectivity pattern stability changes and behavior, some research perspectives suggest that small sample sizes (below 30) reduce statistical power and result stability (Grady et al., 2021). This study's training group had only 16 participants because it examined functional brain changes before and after training. Therefore, caution is needed when interpreting this correlation result and its generalizability. Future research should use larger sample sizes to further investigate the relationship between brain activity changes induced by navigation training and behavior.

In summary, this study used fMRI technology combined with functional connectivity multivariate pattern analysis to examine the cognitive and neural mechanisms underlying improved real-world navigation ability. Task-state functional connectivity results found that navigation training induced a significant increase in the stability of connectivity patterns between the egocentric reference representation core region rSPL and whole-brain voxels, which was significantly positively correlated with behavioral performance in the spatial distance judgment task. The findings support that improvement in real-world navigation ability primarily relies on enhanced egocentric reference spatial representation and further reveal its underlying mechanism. This study also reaffirms that neural pattern stability is an important mechanism underlying learning, and future research can verify this across different learning types to further provide neural indicators for learning goal achievement and learning effect evaluation.

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[1] Due to unequal variances in the independent samples t-test, Mann-Whitney U test was used.

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Note: Figure translations are in progress. See original paper for figures.