

A Scale-Dependent Neural System for Human Spatial Navigation

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Abstract

It is currently unclear whether the human brain processes navigation tasks at different scales in the same way. According to the classical view, humans process navigation information using a hierarchical representation system in a unified way. Other theories, such as the dual and multiple systems theories, suggest that the processing of navigation tasks differs between spatial scales. In addition, previous human navigation studies have mainly focused on scales ranging from rooms to small neighborhoods. However, the neural mechanisms underlying the processing of large-scale spatial navigation tasks in the human brain, and the ways in which neural activation changes with scale, have not been examined in detail. In this study, we conducted a functional magnetic resonance imaging (fMRI) based multi-scale mental navigation experiment across six spatial scales. On the basis of cortical activity patterns, we discovered a scale-dependent neural system that included the parahippocampal gyrus, cingulate gyrus, parietal gyrus and temporal gyrus, revealing neural-based divisions based on spatial scale: small scale (room), medium scale (building), large scale (block), and huge scale (city, country and continent). In contrast, scale-free characteristics were observed in middle occipital gyrus. The current findings provide new insight into the neural mechanisms of scale-driven spatial navigation in humans.

Introduction

The mechanisms by which humans navigate at different spatial scales have been extensively studied over the past several years¹. Understanding the nature of human multi-scale navigation is a critical issue for a range of applications, including navigation system design², spatial ability evaluation^{3,4}, and detection of cognitive impairment, such as preclinical Alzheimer's disease⁵. Classical theories have attempted to elucidate human spatial representations of navigational environments⁶, including unitary^{7,8}, dual^{9,10} and multiple¹¹ systems theories. These theories hold contrary views regarding whether or not internal representations change with spatial scales, leading to the need for further neural-level studies examining scale-dependent and scale-free characteristics that are latent in the neural system and involved in human spatial navigation. A number of previous studies have examined spatial navigation at the small scale (e.g., room, building, town)¹²⁻¹⁴, seeking to understand the spatial processes by which humans perceive, interpret, mentally represent, and interact with spatial characteristics during navigation. Studies of rodents and birds have revealed that different neural mechanisms are involved in spatial navigation between small and large scales¹⁵⁻¹⁷. However, no empirical studies have elucidated the neural mechanisms underlying the performance of large-scale navigation in humans, and how differences in scale drive changes in human brain activation patterns during spatial navigation.

Human spatial navigation involves a range of processes, including visual characteristic processing, spatial distance and direction coding, spatial representation under different reference frames, and route planning. Visual characteristic processing is the basis of spatial navigation, and humans must acquire spatial knowledge to satisfy the information required for self-localization and self-orientation, landmark anchoring and route planning¹⁸. Room, building, and block are the main scales involved in daily

movement for humans in urban environments. At these scales, individuals can directly perceive and process geospatial entities and structures through physical or visual experience¹⁹{Citation}. At the city scale and above, due to the large amount of spatial information and limitations of accessibility and visibility, humans typically cannot intuitively perceive a full picture of geographic space¹¹. Instead, human cognitive processing of large-scale geographic space occurs through indirect learning of spatial knowledge via abstract expressions²⁰. Although human visual processing in spatial navigation has been extensively studied, few studies have examined how the human brain processes scenarios across multiple scales.

In addition to visual feature processing, spatial distance and direction must be coded to measure spatial relationships between two isolated places. Studies examining regional brain activation have shown that the hippocampus and entorhinal cortex are strongly involved in distance processing^{21–24}. In human navigation, Euclidean distances between two objects are reported to be processed in the entorhinal cortex, whereas, when it is necessary to detour, path distances are processed by the hippocampus²¹. For direction processing, besides head direction cells, which can measure spatial direction accurately²⁵, the cingulate gyrus is an important brain region related to direction processing²⁶. A previous study reported that, when humans process directions involving visible objects, the posterior parahippocampal place area (PPA) and retrosplenial complex (RSC) are activated. However, when locating isolated objects that are not in a visible range, such as a gate behind a building, anterior PPA and RSC are activated⁶. The study also explored how humans judge spatial distance across six common scales, revealing cortical gradient processing of spatial information from concrete to abstract⁶. No previous studies have examined how humans process spatial distance and direction during multi-scale navigation.

The reference frame is another fundamental issue in the cognitive neuroscience of spatial navigation. The egocentric system is defined as a viewer-centered perspective, which contributes to external object orientation via deviations in head direction¹⁴. In contrast, the allocentric system is independent of both the viewer and external objects, functioning as a global coordinate system¹⁴. According to small scale navigation studies, both egocentric and allocentric systems appear to represent space in parallel and function complementarily during navigation²⁷. The egocentric system includes viewpoint imagination and mental rotation, and keeps the head direction in accord with the planned route. In contrast, the allocentric system helps an individual orient to unseen or distant objects. To form a reference frame, individuals must obtain sufficient spatial knowledge about the navigation environment. However, as mentioned above, for scales larger than the neighborhood scale, spatial learning using maps differs substantially from spatial learning at smaller scales via real scene perception. Whether there are differences in the use of reference frames between navigation at different scales remains unclear.

In the current study, we hypothesized that the human brain uses a scale-dependent functional system to perform navigation at different scales. The aim of this study was to elucidate how and why differences in scale cause different brain functional activation patterns during spatial navigation. To this end, we tested subjects while they imagined multi-scale navigation, and compared differences in brain activity between

scales. Specifically, we focused on how humans process scenario information and choose spatial references during navigation at different scales.

Results

We compared experimental trials with a baseline condition at the whole-brain level. The results are shown in Figure 1. For room-scale navigation trials, we observed clusters exhibiting significant activation in occipital gyrus, lingual gyrus and medial frontal gyrus. For building-scale navigation trials, we observed clusters of significant activation in the hippocampus, parahippocampus, temporal gyrus, cingulate gyrus, lingual gyrus, frontal gyrus, caudate nucleus, precuneus and calcarine area. For block-scale navigation trials, we observed significant activation in occipital gyrus, lingual gyrus, cingulate gyrus and precuneus. For city-scale navigation trials, we found significant activation in the occipital gyrus, lingual gyrus and temporal gyrus. For country-scale navigation trials, we found significant activation in occipital gyrus and lingual gyrus. For continent-scale navigation trials, we found significant activation in occipital gyrus, lingual gyrus, caudate gyrus and anterior cingulate gyrus.

To investigate which brain regions contribute to scale-driven navigation, we directly compared brain responses during spatial navigation at different scales. The effects of spatial navigation in the brain driven by differences in scale are shown in Figure 2 and 3. Four brain regions exhibited significant differences between scales, namely the parahippocampal gyrus (Figure 2 (a–b)), cingulate gyrus (Figure 2 (c–d)), parietal gyrus (Figure 3 (a–b)) and temporal gyrus (Figure 3 (c–d)) (all $p < 0.05$, AlphaSim corrected). Between the room and building scales, we found greater activation at the building scale in the parahippocampal gyrus, anterior cingulate gyrus and middle temporal gyrus. Between the building and block scales, we found greater activation at the building scale in the parahippocampal gyrus, posterior cingulate gyrus, postcentral gyrus and middle temporal gyrus. Between the building and country scales, we found greater activation at the building scale in the parahippocampal gyrus, anterior cingulate gyrus and posterior cingulate gyrus, whereas greater activation at the country scale was observed in the middle cingulate gyrus, postcentral gyrus and middle temporal gyrus. Between the block and country scales, we found greater activation at the country scale in the postcentral gyrus and middle temporal gyrus. There were no significant differences between the block and city scales, or between the city, country and continent scales. In general, we summarized brain regions on the basis of scale dependency. Figure 4 (a) shows scale-dependent brain regions, including the parahippocampal, cingulate, parietal and temporal gyrus, which exhibited activation that was dependent on changes in the spatial scale of navigation environments. Figure 4 (b) shows the scale-free activation observed in the middle occipital gyrus, which was independent of changes in the spatial scale of navigation environments, but related to navigation tasks.

Discussion

In this study, we identified four scale-related brain activation patterns during the processing of spatial navigation, with significant differences in brain activation patterns across scales. These findings indicate

the existence of unique human navigation strategies at four spatial scales, namely the small scale (between rooms), medium scale (between buildings), large scale (between blocks) and huge scale (between cities, countries and continents). The findings and implications are summarized as below.

First, the results of the comparison between the task and baseline conditions indicated that the middle occipital gyrus was the most important brain region for completing the tasks in this experiment. A previous study reported that the middle occipital gyrus is specialized in processing Chinese characters²⁸. Thus, the observed activation in this region may have been caused by requiring participants to read Chinese words during the experiment. However, another study reported that activation in the middle occipital gyrus was strongly related to successful navigation²⁹. In addition, some previous research suggests that the middle occipital gyrus is involved in object processing³⁰⁻³², indicating that participants processed knowledge of landmarks located in the navigation scenarios. Furthermore, the middle occipital gyrus is also reported that it plays a role in processing objects at different levels of specificity³³, suggesting that participants processed landmarks at different scales with the involvement of the middle occipital gyrus, and that the specification of processed landmarks is dependent on the scale of the navigation scenario. Taken together with these previous findings, the current results suggest that the middle occipital gyrus is a scale-free brain region for human navigation.

The parahippocampal gyrus is an important brain region in spatial processing. The results indicate that activation of the parahippocampal gyrus at the medium scale was significantly greater than that at the small and larger scales. The parahippocampal gyrus is considered to play an important role in view encoding in spatial navigation, particularly for views of buildings³⁴, which may have caused the greater activation observed at the building scale in the current study. Hassabis et al. reported that activation in the parahippocampal gyrus discriminated between different environments³⁵, in accord with the current results, suggesting that the medium scale is a key demarcation in human spatial navigation. These studies provide evidence suggesting that the parahippocampal gyrus discriminates between processing views at different spatial scales. Moreover, the parahippocampal gyrus was reported to be involved in the process of perceiving and using landmarks¹⁸, and was strongly activated when participants attempted to increase navigational accuracy³⁶. The current findings suggest that participants paid substantially more attention to retrieving and reusing landmarks based on their memory of routes to complete navigation tasks at the medium scale. In addition, the parahippocampal gyrus is considered to be responsible for the processing of global information about the environment in humans³⁷, receiving egocentric information and converting it to allocentric representations, and helping navigation in an allocentric view^{36,38}. The current findings suggest that participants tended to use an allocentric reference to complete the navigation tasks.

The cingulate gyrus is also a scale-dependent brain region. We found significant differences in anterior cingulate gyrus activation between the medium and huge scales, but not between the small and large scales. Previous studies reported that the anterior cingulate gyrus is related to backtracking strategy³⁹. The anterior cingulate gyrus is also reported to exhibit more activation when participants experience

difficulties in navigation tasks³⁶. Therefore, our findings suggest that participants experienced more difficulty and performed more backtracking at the small to large scales. In contrast, at the huge scale, navigation appeared to be easier and more direct. We also found significant differences in posterior cingulate gyrus activation between the medium scale and above, but no differences between the small and medium scales. The posterior cingulate gyrus is thought to be involved in transforming allocentric references to egocentric references⁴⁰. The current findings and our oral investigation of the route training sessions indicate that, at the small to large scale, participants tended to imagine an abstract structure of the entire environment using an allocentric reference. In addition, at the small to medium scales, participants also switched spatial references frequently. Thus, participants may have been imagining real processes of navigation and processing local information with an egocentric reference.

Activation was influenced by spatial scale in several other brain regions. First, we found a scale-dependent difference in activation in the parietal gyrus. The results indicated that activation in parietal gyrus increased monotonically with spatial scale, in accordance with a previous report by Peers et al. that stated that the parietal gyrus exhibited more activation at large scales⁶. The parietal gyrus is involved in processing egocentric references^{41,42}. Therefore, our findings suggested that, at the huge scale, participants completed navigation by imagining maps in an egocentric reference frame, in which routes were simplified on the basis of the paths of flights or ships. Second, we found that the temporal gyrus was strongly activated at the huge scale. The temporal gyrus is related to the processing of spatial contextual information for route planning, and distinguishing between navigational episodes⁴³. Some previous studies examining spatial navigation among patients with Alzheimer's disease suggested that patients suffered from spatial disorientation due to neurodegeneration in the medial temporal gyrus and parietal gyrus⁴⁴⁻⁴⁷. In addition, several studies reported that the parietal gyrus is related to the processing of direction^{41,48}. Therefore, although participants were able to easily plan and navigate along a route, they may have found it harder to determine accurate directions because they naturally retrieved and processed fewer details about the environment compared with the small to large scales.

At all of the scales we investigated, we observed a scale-dependent neural system for human spatial navigation, and there are four typical scale-dependent brain activation patterns and corresponded navigation strategies. In the current study, at the small scale, participants used both egocentric and allocentric references, but processed real and detailed scenario views more, indicating that participants mainly used egocentric references during navigation. At the medium scale, participants used both egocentric and allocentric references, with no obvious differences, and tended to switch reference type frequently to cope with different scenarios during a single navigation task. Participants processed both specific landmark information and abstract route networks. This type of navigation strategy enabled participants to process information comprehensively and navigate more accurately, but also naturally led to a higher level of difficulty in completing tasks. At the large scale, participants mainly used an allocentric reference and processed abstract spatial information, because the amount of information at this spatial scale was overly large for participants to process, and they had to rely on abstract information by simplifying the spatial information into route networks and several key decision points. At

the huge scale, participants mainly used an egocentric reference to process undetailed and abstract mental maps. Our findings are consistent with the multiple system theory for spatial representation¹¹, and also verify the fact that human activate a specific neural system⁶ to accomplish different navigation strategies proper to spatial scales⁴⁹.

In conclusion, the current study provided whole-brain, voxel-based evidence supporting the role of various brain regions in scale-driven spatial navigation. The current results revealed, for the first time, a scale-dependent neural system that included the parahippocampus, cingulate, parietal and temporal gyrus, and revealed a neural-based division of spatial scale: small scale (room), medium scale (building), large scale (block), and huge scale (city, country and continent). These four scales were associated with obvious differences from the perspective of spatial information processing and spatial referencing, revealing the neuronal basis of the influence of scale on human navigation and spatial cognition. In addition, activity in the middle occipital gyrus was found to be independent of scale in human spatial navigation. Furthermore, this finding provides potentially useful information regarding the design of auto-adapted navigation systems for multi-scale navigation, contributing to the investigation of novel methods for detecting preclinical Alzheimer's disease via multi-scale navigation tests.

Methods

Subjects.

We recruited 11 human subjects (five males, aged 19–24 years) for the experiments. All of the subjects were Chinese undergraduate or graduate students at universities in Beijing, China. All subjects had a high level of education and had good navigation skills. Four subjects majored in geography or geography-related subjects. All of the subjects were trained in navigation tasks before fMRI scanning. All subjects provided written informed consent before the experiment. All experimental procedures were performed in accordance with the Declaration of Helsinki. The experiment was reviewed and approved by the Beijing Normal University Research Ethics Committee.

Experimental stimuli.

Location pairs were used as experimental stimuli, which were displayed as text on the screen during scanning. Six scales were set as the conditions of the experiment, including room, building, block, city, country and continent, in accordance with a previous study. All of the location pairs comprised two locations at the same scale. For example, at the room scale, we used the room names as the location pairs. Similarly, for the building scale and the block scale, we used the building names and the block names, respectively. For scales larger than block, including the city, country and continent scales, city names were used for the location pairs, such as “Beijing, Shanghai” at the city scale, “Beijing, Tokyo” at the country scale, and “Beijing, London” at the continent scale. Training experiments were conducted before the formal navigation experiment to test whether all subjects were familiar with these locations.

The location pairs were displayed with a top-bottom layout. The starting points were located at the top and the end points were located at the bottom.

Experimental paradigm:

The experimental task required subjects to plan a route on the basis of the displayed location pair, and to imagine themselves navigating the planned route. The fMRI experiment conformed to a randomized block design paradigm. Each block lasted 12.5 s followed by a 7.5 s fixation period. In each block, the stimuli were displayed, and subjects began the navigation task. Subjects stopped the task once they saw a fixation cross. The experiment included four runs, and each run comprised 24 blocks (four blocks per scale condition).

MRI acquisition:

The fMRI scans were conducted using a 3-Tesla Siemens scanner (Siemens Trio, ***). The acquisition parameters were as follows: repetition time (TR), 2,500 ms; echo time (TE), 30 ms; flip angle, 90°; field of view, 204 mm; matrix size, 68 × 68; functional voxel size, 3 × 3 × 3 mm; 46 slices, interleaved acquisition order, no gap; 200 TRs per run. In addition, T1-weighted high resolution (1 × 1 × 1 mm) scanning was performed.

Statistical analysis.

SPM 12 was used for statistical analysis of fMRI data. First, we conducted individual-level analysis using the general linear model to estimate the beta values of different contrasts between scales. Blood-oxygenation-level-dependent signals were averaged for all blocks containing each scale across all runs. Second, we conducted one-sample t-tests for group level analysis. Beta plots were also created by averaging the beta values calculated in the random-effects general linear model analysis across all subjects.

Declarations

Data availability.

All the material will be available on request from the corresponding author.

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Author contributions

W.D. and S.W. designed the research. S.W. collected and analysed the data. S.W. prepared the figures and wrote the main manuscript text. All authors reviewed the manuscript.

Competing Interest Statement

The authors declare no conflict of interest.

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Figures

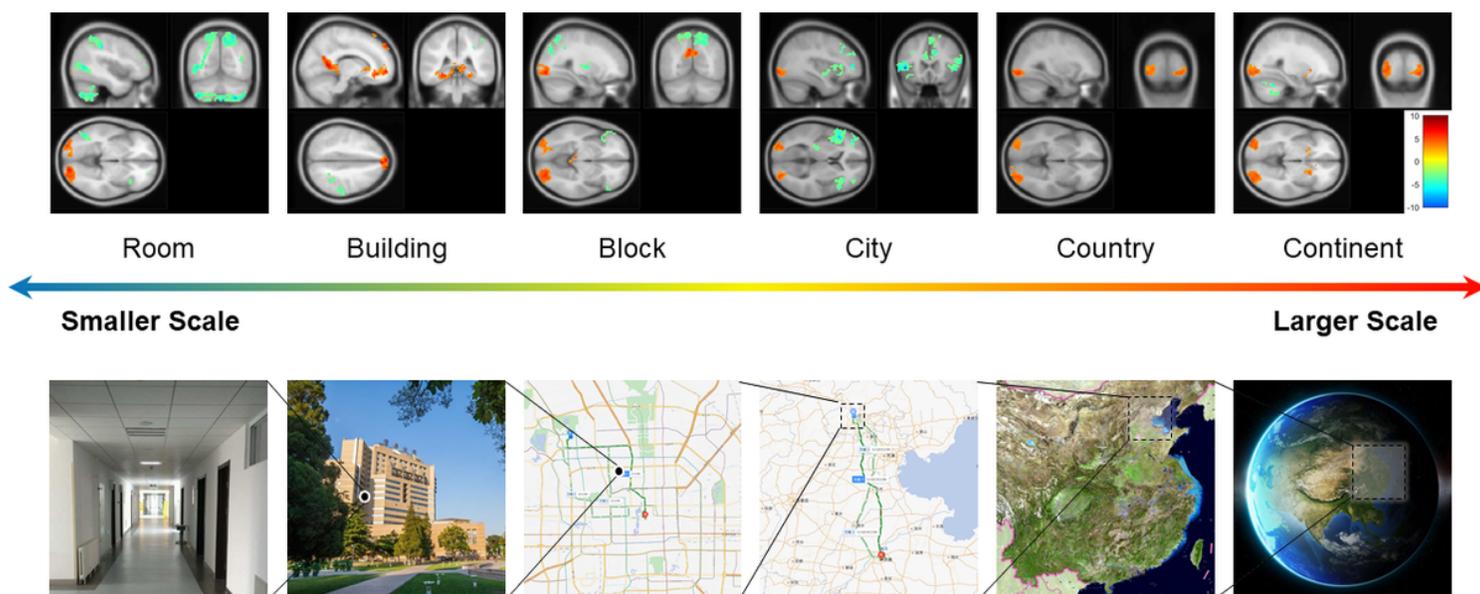


Figure 1

Activation (red) and deactivation (blue) in the human brain during multi-scale geospatial navigation task, compared with the baseline condition.

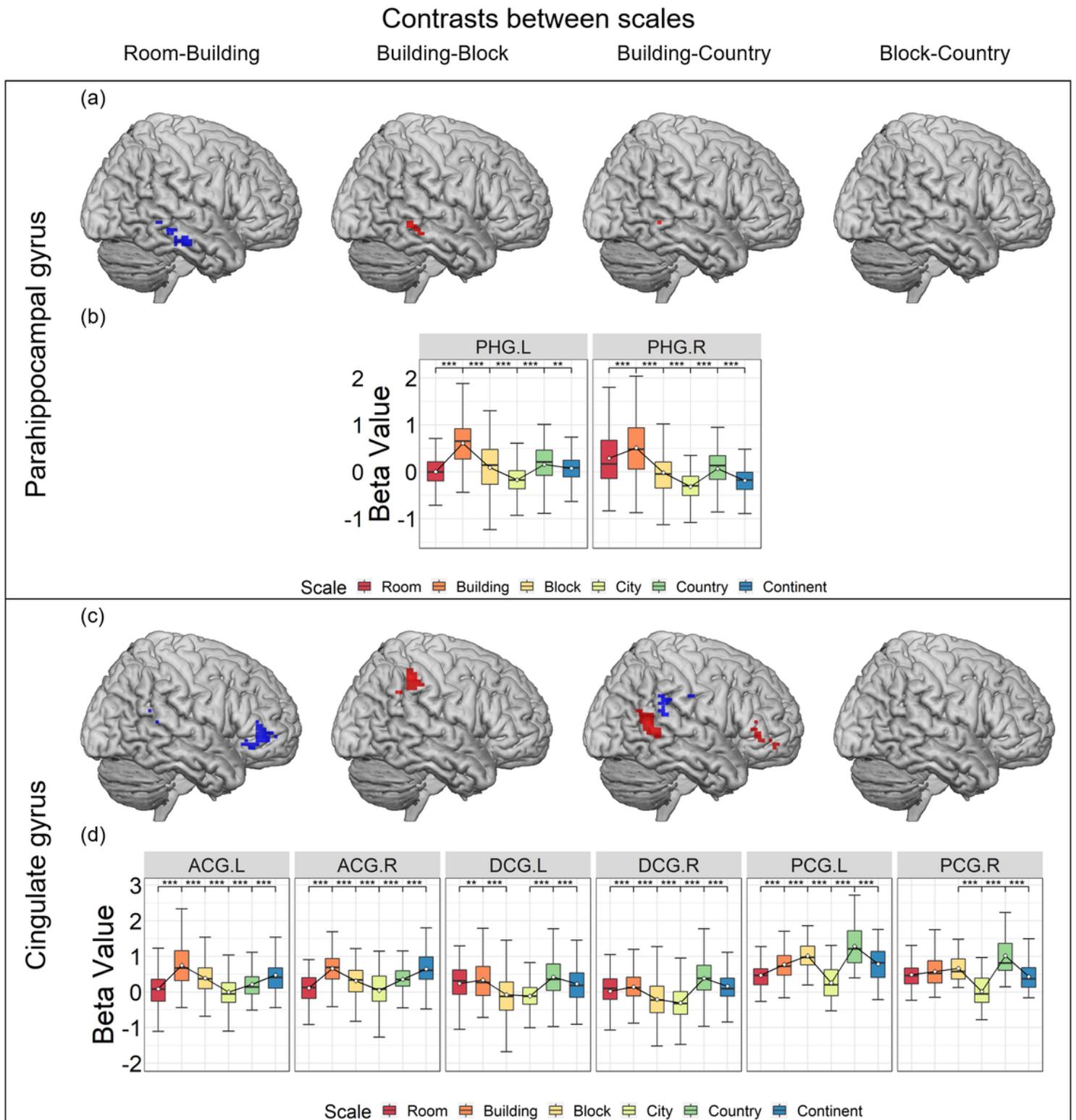


Figure 2

Activation and deactivation of parahippocampal and cingulate gyrus comparing between multi-scale spatial navigation tasks and ROI-based statistics for the difference of beta values (activated regions are marked in red, and deactivated regions are marked in blue. Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). (a) Activation and inactivation of parahippocampal gyrus; (b) Statistics for the difference of beta values in bilateral parahippocampal gyrus (PHG); (c) Activation and inactivation of cingulate gyrus; (d)

Statistics for the difference of beta values in cingulate gyrus including bilateral anterior (ACG), median (DCG) and posterior (PCG) cingulate gyrus, middle (MTG) and inferior (ITG) temporal gyrus.

Contrasts between scales

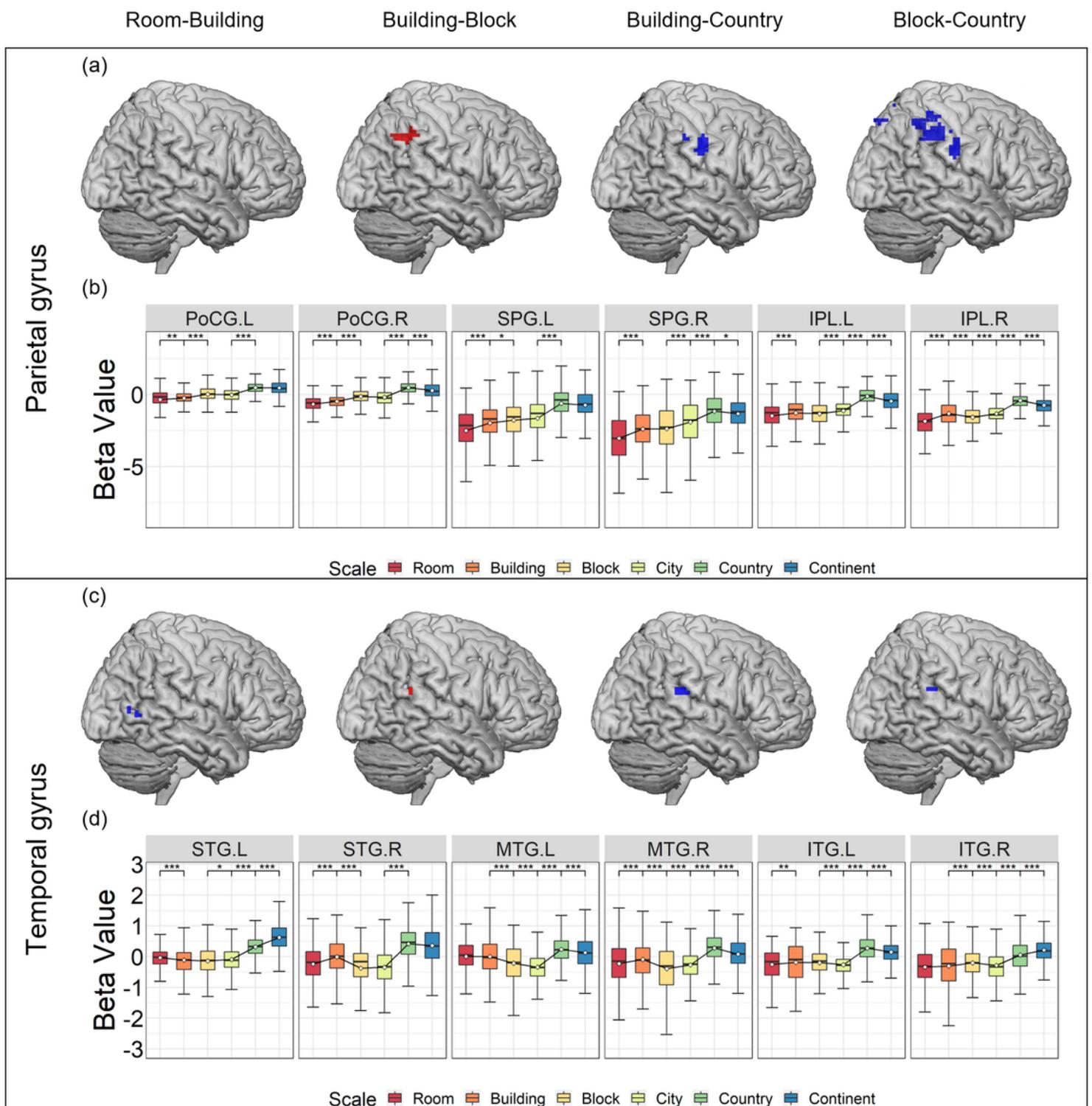


Figure 3

Activation and deactivation of parietal and temporal gyrus comparing between multi-scale spatial navigation tasks and ROI-based statistics for the difference of beta values (activated regions are marked in red, and deactivated regions are marked in blue. Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). (a)

Activation and inactivation of parietal gyrus; (b) Statistics for the difference of beta values in parietal gyrus including bilateral postcentral gyrus (PoCG), superior parietal gyrus (SPG) and inferior parietal gyrus (IPL); (c) Activation and inactivation of temporal gyrus; (d) Statistics for the difference of beta values in temporal gyrus including bilateral superior (ATG), middle (MTG) and inferior (ITG) temporal gyrus.

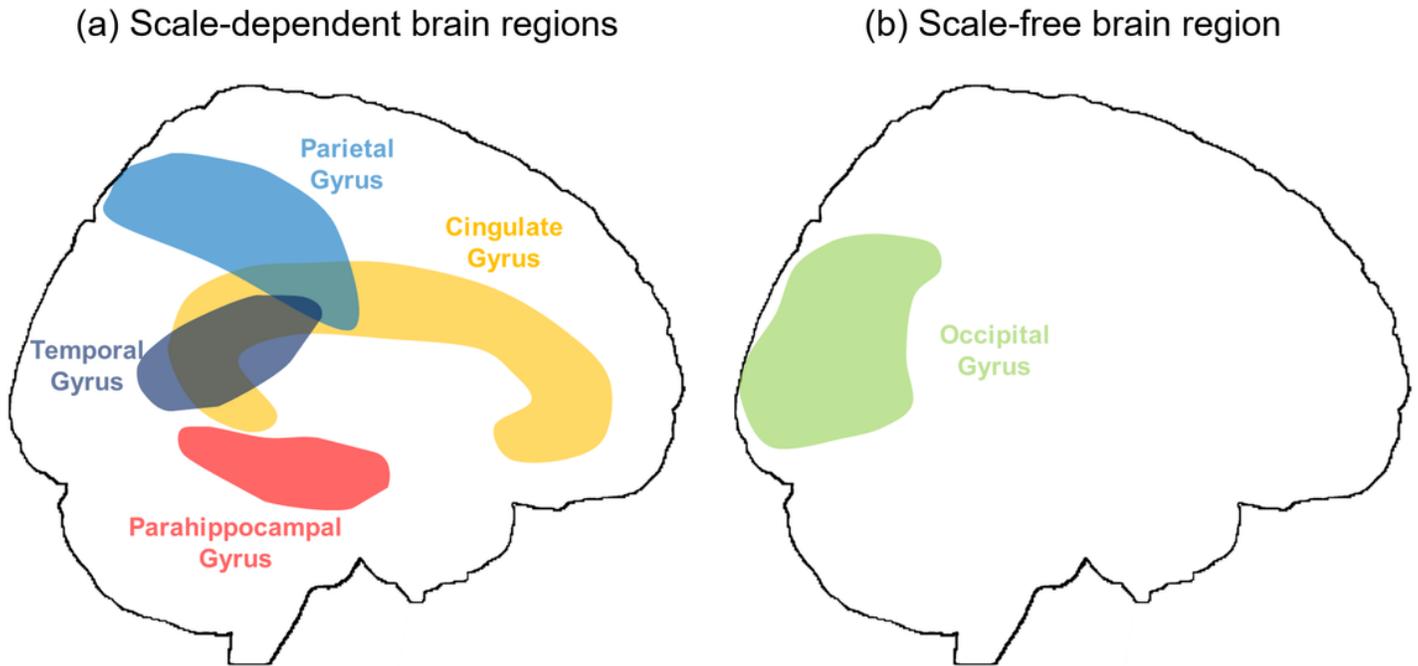


Figure 4

Summarized brain regions based on scale dependency. (a) Scale-dependent brain regions including parahippocampal, cingulate, parietal and temporal gyrus, which exhibited activation that was dependent on changes in the spatial scale of navigation environments; (b) Scale-free activity in a brain region including the middle occipital cortex, which was independent of changes in the spatial scale of navigation environments, but was related to navigation tasks.