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Summary

In many non-human species, neural computations of navigational information such as position and orientation are not tied to a specific sensory modality [1, 2]. Rather, spatial signals are integrated from multiple input sources, likely leading to abstract representations of space. In contrast, the potential for abstract spatial representations in humans is not known, as most neuroscientific experiments on human navigation have focused exclusively on visual cues. Here, we tested the modality independence hypothesis with two fMRI experiments that characterized computations in regions implicated in processing spatial layout [3]. According to the hypothesis, such regions should be recruited for spatial computation of 3-D geometric configuration, independent of a specific sensory modality. In support of this view, sighted participants showed strong activation of the parahippocampal place area (PPA) and the retrosplenial cortex (RSC) for visual and haptic exploration of information-matched scenes but not objects. Functional connectivity analyses suggested that these effects were not related to visual recoding, which was further supported by a similar preference for haptic scenes found with blind participants. Taken together, these findings establish the PPA/RSC network as critical in modality-independent spatial computations and provide important evidence for a theory of high-level abstract spatial information processing in the human brain.

Results

To test our hypothesis that the human brain would show modality independent responses to spatial layout, we used fMRI while presenting participants with a modified version of a paradigm previously shown to activate scene sensitive regions in sighted humans [4].

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Specifically, we used Lego bricks to construct (i) 27 indoor scenes that were matched in size and complexity but differed with respect to their geometric properties and (ii) 27 abstract geometric objects. We then administered a delayed matching-to-sample (DMTS) task that required participants to compare the spatial layout of four sequentially presented stimuli to a final sample stimulus (Figure 1). This behavioral task was administered separately in two versions, a visual version during which subjects saw grayscale photographs of the stimuli and a haptic version during which they acquired the geometric structure of the stimuli via exploration with the right hand.

Spatial layout processing in sighted subjects

While reaction times in the visual version of the DMTS task did not differ between objects and scenes ($p > 0.5$), the PPA (identified in each subject with a functional localizer, see Supplemental Experimental Procedures) responded more vigorously when subjects were attending to the geometric structure of indoor scenes than objects ($t = 10.22$, $p < 0.001$, $d = 1.92$; Figure 2A). Importantly, activation differences between objects and scenes did not correlate with differences in reaction time (left PPA: $r = .21$, $p > .5$; right PPA: $r = -.64$, $p > .1$) or accuracy (left PPA: $r = .29$, $p > .5$; right PPA: $r = .63$, $p > .1$), and they did not differ between the right and left PPA ($F = 4.108$, $p = 0.09$, condition by hemisphere interaction: $F = 0.437$, $p = 0.533$). These results replicate previously reported differences between Lego scenes and objects in the PPA during passive viewing and during a continuous one-back task [4]. Voxel-wise whole-brain analyses revealed similar effects in RSC and in the superior frontal gyrus (Table S1). By comparison, the reverse contrast (objects > scenes) did not reveal any significant results, and we did not observe any voxels that showed a significant correlation with behavioral performance.

In the haptic version of the DMTS task, reaction times also did not differ between the two stimulus types ($p > 0.05$), and we observed significantly stronger responses in the PPA when subjects explored the scenes by touch as compared to the objects ($t = 2.45$, $p < 0.05$, $d = 0.40$; Figure 2A). Again, larger activation differences between scenes and objects were not associated with larger differences in reaction time (left PPA: $r = -.32$, $p > .4$; right PPA: $r = .25$, $p > .5$) or accuracy (left PPA: $r = -.59$, $p > .1$; right PPA: $r = -.02$, $p > .5$), and treating the right and left PPA as separate regions of interest (ROI) did not reveal a main effect of hemisphere ($F = .009$, $p = 0.93$) nor an interaction between task and hemisphere ($F = 1.753$, $p = 0.23$). These results demonstrate that coding for spatial layout in the PPA can be driven by modalities other than vision. In addition, because the match and sample stimuli differed with respect to the presence of furniture and toy characters (see Supplemental Material), we reran our analyses while only focusing on the sample stimuli. These analyses replicated all the results reported for the sighted and the blind participants (see below); hence, only the results from the analyses that included the match stimuli are reported here.

Given that (i) haptic experiences can be recoded into visual mental images [5] and (ii) visual imagery of scenes can elicit both occipital and PPA responses [6], the PPA responses we observed during haptic exploration could, in principle, reflect a visual representation of scene geometry. Visual information reaches the posterior parahippocampus via direct projections from multiple occipital regions [7, 8], hence we addressed this *recoding hypothesis* with functional connectivity analyses. Specifically, for both DMTS tasks, we tested whether occipital regions showed a scene-specific increase in coupling with the PPA (collapsed across hemispheres). In contrast to the visual task, we did not observe any significant voxels in the haptic task, indicating that the covariation between occipital and PPA responses did not differ between scene and object blocks during haptic exploration. Direct comparisons supported these findings by revealing multiple clusters in occipital cortex in which the scene-related increase in coupling with the PPA was significantly stronger under visual than haptic stimulation (Figure 2B, Table S2).

Spatial layout processing in blind subjects

Experiment 1 suggests that scene selective responses in the human brain can be driven by modalities other than vision. Given the absence of context-dependent coupling between occipital cortex and the PPA during haptic exploration, these results are unlikely to arise from occipital processing during non-visual stimulation, which would have been indicative of mental imagery. However, because occipital activation has not always been reported in studies on mental imagery [9], we performed a second, complementary test of the recoding hypothesis with age and gender matched blind participants. Analogous PPA/RSC involvement in the blind participants would rule out the possibility of recoding based on visual experience and provide evidence for multimodal processing of spatial layout.

Like the sighted participants, those who were blind responded as quickly to scene stimuli as to objects (p>0.1). Since a paradigm to localize the PPA in blind subjects has yet to be established, we followed a previously established approach [10] and used the group results from the functional localizer task in the sighted subjects to define an average PPA ROI for the blind participants (Figure 3). As Figure 3 demonstrates, activation profiles in the blind participants were highly similar to the sighted: BOLD responses were significantly greater when subjects haptically explored the scenes than when they explored objects (t=4.19, p<0.01, d=0.62) but did not differ between the right and left PPA (main effect of hemisphere: F=0.07, p=0.80; task by hemisphere interaction: F=1.26, p=0.30). Moreover, differences in BOLD responses did not correlate with differences in reaction time (left PPA: r=−.32, p>.4; right PPA: r=.32, p>.4) or accuracy (left PPA: r=.54, p>.2; right PPA: r=.13, p>.5). Outside the PPA, both groups showed stronger bilateral activation for haptic exploration of scenes in RSC (Figure 4, Table S1); however, in the left hemisphere, the cluster of significant voxels extended into the parieto-occipital sulcus. Similar results were observed in area 7p [11] of the superior parietal lobe and in the middle frontal gyrus. As the RSC appeared to show deactivation for objects in the blind subjects, we tested for a negative effect but did not observe any significant voxels, neither in the sighted nor the blind subjects. Importantly, we did not observe differences between scenes and objects in primary motor cortex, suggesting that the amount of motor exploration did not differ between stimuli. Furthermore, the reverse analysis (objects > scenes) did not reveal any significant effects, and we did not observe any voxels that showed a significant correlation with behavioral performance.

Finally, we tested for overlapping and differential responses between sighted and blind participants with a whole-brain analysis on the haptic task. A conjunction analysis [12] revealed that both blind and sighted participants recruited a large network of regions during haptic exploration of scenes and objects, with the maximum responses in areas implicated in motor control and sensorimotor processing (Table S5). In addition, although blind and sighted subjects did not differ in their overall reaction times (F=0.054, p>0.5), blind subjects exhibited stronger activation in occipital and middle temporal areas (Table 2). These findings support previous reports showing that blind humans recruit occipito-temporal cortices during tactile exploration of objects [13, 14] and Braille reading [15, 16]. However, similar to the sighted participants, a functional connectivity analysis did not reveal any clusters in occipital cortex that showed a stronger covariation with the PPA during scene than during object blocks.

Discussion

These studies investigated whether regions such as the PPA and the RSC can be recruited for computation of spatial layout, independent of a specific sensory modality. In experiment 1, sighted subjects showed stronger PPA/RSC responses for visually presented scenes than for objects, which replicates previous findings. Similar differences were observed when

stimuli were apprehended via haptic exploration, suggesting a targeted network that can be driven both by visual and non-visual spatial information. Importantly, functional connectivity analyses and a similar PPA/RSC preference for scenes in blind participants showed that these effects were not related to a recoding of haptic experiences into visually dependent mental images. Taken together, our findings strongly support a theory of modality-independent coding of spatial layout in the brain, which adds to the growing evidence for multimodal coding in other specialized processing regions such as the fusiform face area [17, 18] or the object-sensitive ventral visual pathway [10, 19].

Although previous research on the spatial functions of the PPA and RSC has focused on visual processing, spatial information can be acquired and represented from multiple non-visual sources [20]. For example, in rodents, position signals in place and grid cells, and orientation signals in head direction cells, are not only sensitive to visual landmarks but can also be updated by body-based cues when the animal moves around in darkness [1, 2]. In addition, human behavioral studies suggest that both visual and nonvisual cues influence our navigational behavior [21–24]. Taken together, this evidence indicates that various types of spatial information can be acquired from different sensory modalities and ultimately represented in a common, modality-independent format, thus supporting mental computations and spatial behaviors independent of the input source. This hypothesis has been elaborated in several ways, including the spatial representation system [25], the spatial image [26], and the notion of metamodal brain organization [27].

The present results extend this claim by showing that the scene specific responses in the human brain are not restricted to visual input, but can also arise from haptic exploration. Our findings are parallel to those of Mahon et al. [10] who showed that preferences for object categories in the ventral visual stream do not require visual experience. Here, when scenes and objects were presented as grayscale photographs to the sighted subjects, we observed the well-established PPA preference for scenes. When corresponding information was acquired from haptic exploration of the physical models, a similar PPA preference for scenes emerged. Although this effect could have been driven by a recoding of haptic experiences into visual mental images, this account appears unlikely for two reasons. First, the coupling between occipital cortex and the PPA was selectively enhanced during visually presented scene blocks, which argues against an imagery-related occipital contribution. Second, we observed the same PPA selectivity for scenes in blind participants during haptic exploration. Although the definition of the PPA in the blind bears some anatomical uncertainty – due to the absence of an established functional localizer for this population – our data suggest that the PPA intrinsically functions to represent spatial layout in a format that is not tied to a specific sensory modality.

In addition to the PPA, we observed stronger responses to scenes in RSC, independent of the encoding modality. Although several proposals exist with regard to the precise navigational functions of the RSC [28–30], our tasks are fully consistent with studies reporting strong RSC responses to unfamiliar scenes that provide ample geometric information [29]. Our results show for the first time, that scene sensitivity in the RSC, as in the PPA, is not restricted to the visual modality but that it also emerges when spatial layout information is acquired from haptic experiences. Given the extensive network of afferent projections to the RSC [31], it therefore appears likely that various streams of spatial information processing converge in the RSC to support the encoding, storage, and manipulation of spatial layout information.

Both in the PPA and the RSC, the overall activation and the scene specific increases were weaker in the haptic than in the visual condition. These differences are likely related to differences in sensory processing: haptic input is slower to apprehend, due to serial vs.

parallel encoding, and tactile resolution and bandwidth capacity is far lower than that of vision [32]. As such, one would expect it to be a slower and noisier signal to use for building up a scene representation. Behavioral findings support this assumption, because visual maps are faster to learn and yield less overall variability at test than the same learning/testing from haptic maps, but both input modalities show an almost identical pattern of speed and error performance on spatial updating tasks [33]. These results indicate the building up and accessing of a multimodal representation, which is consistent with our findings of the PPA and the RSC processing information from multiple input sources. Importantly, future studies – potentially using intracortical recordings – are needed to ultimately verify the idea that identical neuronal populations are driven by visual and haptic inputs.

In conclusion, we have shown that the PPA and the RSC, two key regions of the human spatial navigation network [34], respond both to visual and haptic presentation of spatial layouts. Together with the multisensory properties of other spatial systems such as the head direction, grid and place cell networks, our findings provide further evidence for the notion that the mammalian brain may code for spatial information in a format that is not tied to a specific sensory modality. Given that spatial properties (size, distance, direction etc.) are fundamental dimensions of the physical world that do not require a specific type of sensory processing, it is tempting to speculate that cortical systems have evolved to construct this abstract format.

Experimental Procedures

Subjects

Eight healthy volunteers (six right-handed and one ambidextrous according to [35], one unknown), all with normal or corrected-to-normal vision, participated in Experiment 1, and eight blind volunteers (all right-handed Braille readers), matched for age and sex, participated in Experiment 2. Because one blind participant in experiment 2 had to be removed due to excessive head movement, we removed the corresponding sighted subject as well. Therefore, the final data sets comprised seven sighted subjects (2 female, age range: 22–77 yrs) and seven blind subjects (2 female, age range: 22–75 yrs). See Table S3 for further information on the etiology and age of onset of blindness.

Image processing and statistical analysis of fMRI data

Image processing and statistical analysis were carried out using SPM8 (Wellcome Department of Imaging Neuroscience, London, UK). All volumes were realigned to the first volume, spatially normalized to an EPI template in a standard coordinate system [36] and finally smoothed using a 9 mm full-width at half-maximum isotropic Gaussian kernel.

In the sighted subjects, we identified the PPA in each subject with a functional localizer task (see Supplemental Experimental Procedures). We also performed a whole-brain fixed effects analysis across all sighted subjects to define a PPA-ROI for the blind subjects, given the absence of an established PPA localizer for this population. We then estimated statistical models for the DMTS tasks in the PPA-ROI's of each participant and entered the resulting parameter estimates into paired t-tests. To test for regions outside the PPA showing differences between objects and scenes, we performed random effects whole-brain analyses as implemented in SPM8.

The functional connectivity analyses were performed with the functional connectivity toolbox (web.mit.edu/swg/software.htm) – one for the visual and one for the haptic condition – to identify voxels in occipital cortex whose activation showed a stronger covariation with the PPA during scene than during object blocks. Detailed information about

experimental procedures, MRI acquisition, image processing, and statistical analysis of fMRI data are given in the Supplemental Experimental Procedures.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Highlights

- The Parahippocampal Place Area (PPA) and Retrosplenial Cortex (RSC) support computations of spatial layout, independent of whether the information is acquired from vision or touch

- Computation of spatial layout in the PPA/RSC were observed both in sighted and in congenitally/adventitiously blind humans

- Non-visual spatial layout computations in the PPA/RSC network are unlikely to be driven by visual mental imagery
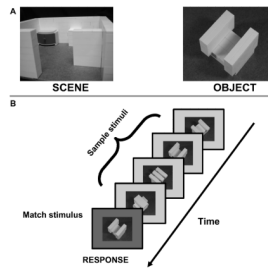
Figure 1. Experimental paradigm of the delayed matching to sample task

(A) We constructed 27 scenes and 27 objects with different geometric layouts. To make the rooms distinguishable, we manipulated the number, size, and position of the interior walls, thereby giving each room a unique geometric layout. Because the PPA is believed to represent navigable spatial layouts in which one can move about [2], the scenes also contained toy characters and small furniture. In addition, we acquired digital images of each room and each object and rendered them in grayscale. In the visual condition, stimuli were displayed as photographs on a screen inside the bore of the MRI scanner. Six blocks of objects and six blocks of rooms were presented in alternating order, with intervening rest periods (duration: 16s) during which subjects fixated a white cross on a black background. In the haptic condition, the physical models were placed on a tray positioned on the upper right thigh, and participants explored the stimuli with the right hand. For further information about the stimuli, see Figure S1.

(B) Each trial started with the presentation of four sample stimuli, followed by a fifth stimulus, the match stimulus (shown here for the object scenario). In the case of scenes, furniture was removed from this final match stimulus to emphasize that the geometric properties were the relevant dimension. In the visual task, each image was shown for 3s, followed by a 1s interstimulus interval (ISI). In the haptic task, each stimulus was presented for 12s, followed by a 4s ISI. Participants decided with a two alternative forced choice button press whether or not the geometric structure of the match stimulus was identical to any of the previous four sample stimuli. Six blocks of objects and six blocks of rooms were presented in alternating order, with the initial block type randomized across participants.
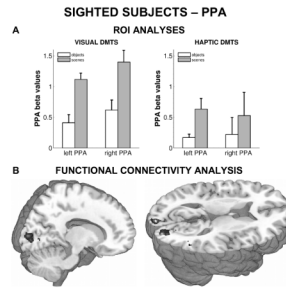
Figure 2. Modality independent scene processing in the PPA of sighted subjects
(A) In the visual version of the delayed matching to sample task, the PPA responded more strongly when subjects were viewing and memorizing scenes as compared to objects (left). Similar results were observed in the haptic condition (right) when subjects manually explored the stimuli. For each subject and condition, we extracted the responses for scenes and objects and averaged them across all voxels in the individual PPA regions of interest (as identified by the functional localizer). The graph shows the mean activations (+SEM) in the PPA averaged across participants. Effect sizes for the differences between scenes and objects were as follows: Visual DMTS: left PPA (d=1.68), right PPA (d=1.57); Haptic DMTS left PPA (d=1.21), right PPA (d=0.29). See Table S1 for additional whole-brain analyses and Figure S2 for data from individual subjects.
(B) Given that the PPA receives direct projection from various occipital areas, we performed functional connectivity analyses with the PPA as a seed region to identify voxels whose activation showed a stronger covariation with the PPA during scene than during object blocks. After performing this analysis separately for the visual and the haptic DMTS task, a paired t-test revealed multiple clusters in occipital cortex in which the context dependent coupling was significantly stronger during visual than during haptic stimulation. To show the subthreshold extent of the effect, results of the random effects analysis are displayed on the MNI template brain with a threshold of p<.001 uncorrected. See Table S2 for complete voxelwise statistics.
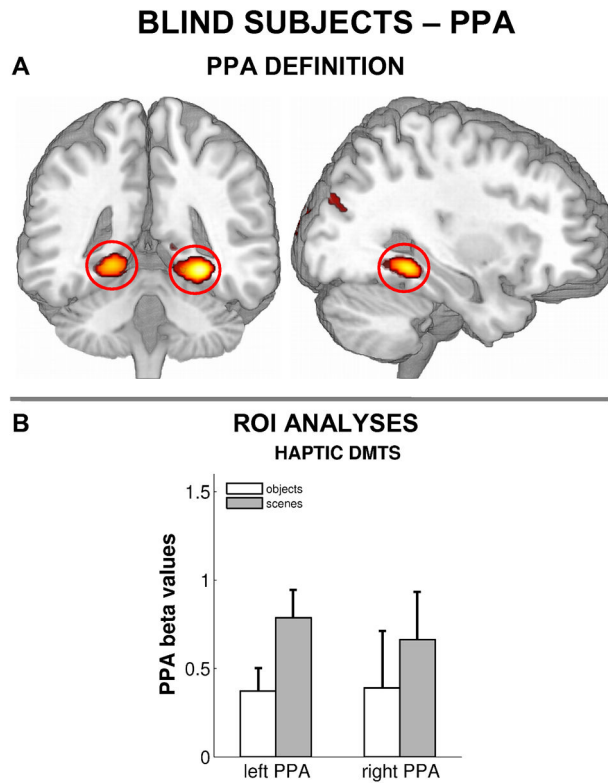
BLIND SUBJECTS – PPA

A **PPA DEFINITION**

B **ROI ANALYSES**
HAPTIC DMTS

Figure 3. Haptic scene processing in the PPA of blind subjects

(A) Given the absence of a functional PPA localizer for blind subjects, we defined the PPA based on the results from the functional localizer task in sighted subjects. The panels show the results of a fixed effects analysis in the sighted subjects that tested for differences between scenes and objects. Results are displayed on the MNI template brain, using a threshold of p<.05 corrected for multiple comparisons. For each of the blind subjects, we extracted the responses for scenes and objects and averaged them across all voxels in the right/left PPA.

(B) In the haptic version of the task, blind participants showed stronger PPA activation for scenes than for objects, thus replicating the results of the sighted subjects. The graph shows the mean activations (+SEM) in the PPA-ROI's, averaged across participants. Effect sizes for the differences between scenes and objects were as follows: left PPA (d=1.04), right PPA (d=0.28). For detailed demographic data on the blind participants, see Table S3.
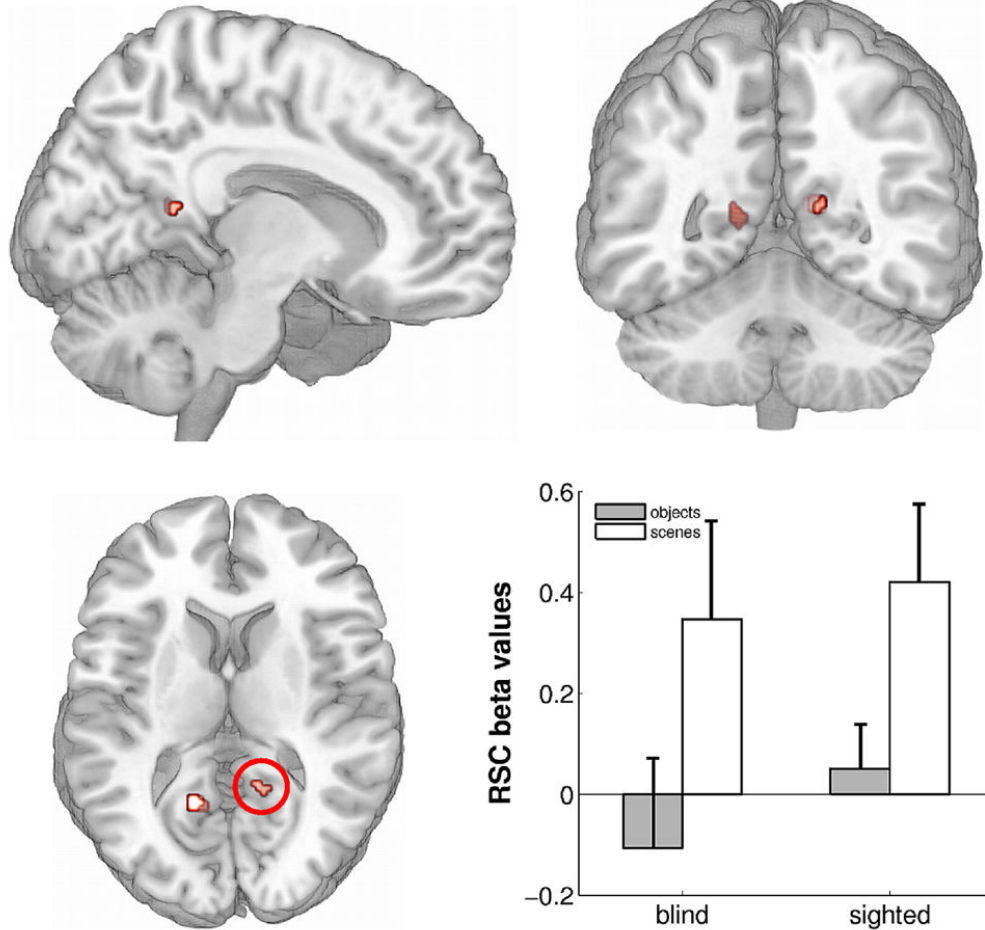
HAPTIC DMTS - WHOLE BRAIN ANALYSIS

Figure 4. Haptic scene processing in retrosplenial cortex
Whole brain analysis showing regions beyond the PPA that responded more strongly to haptic exploration of scenes than objects in both groups. Consistent with our findings on visual processing, bilateral effects were observed in retrosplenial cortex, and scene selectivity did not differ between blind and sighted participants. In all panels, results of the random effects analysis are displayed with a threshold of p<.05 corrected for multiple comparisons. The lower right panel shows the mean activations (+SEM) of all voxels in the right retrosplenial cortex, averaged across participants. Similar results were obtained in superior parietal cortex and middle frontal gyrus (see Table S4). For further activations common to both subject groups, see Table S5. For signal time courses from the RSC and the PPA see Figure S4.