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## Parahippocampal and retrosplenial contributions to human spatial navigation

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### Abstract

Spatial navigation is a core cognitive ability in humans and animals. Neuroimaging studies have identified two functionally-defined brain regions that activate during navigational tasks and also during passive viewing of navigationally-relevant stimuli such as environmental scenes: the parahippocampal place area (PPA) and the retrosplenial complex (RSC). Recent findings indicate that the PPA and RSC play distinct and complementary roles in spatial navigation, with the PPA more concerned with representation of the local visual scene and RSC more concerned with situating the scene within the broader spatial environment. These findings are a first step towards understanding the separate components of the cortical network that mediates spatial navigation in humans.

### Introduction

The ability to find one's way through a large-scale space such as an airport, college campus, or city neighborhood is essential for successful functioning in the modern world. Wayfinding was probably even more important to our phylogenetic ancestors, who could not have survived without the ability to navigate between locations that provided food, shelter, and water. Neurophysiological studies in animals have significantly advanced our understanding of how this core cognitive function is implemented at the neuronal level by identifying several classes of cells that encode spatial quantities useful for navigation, including place cells in the hippocampus [1], head direction cells in Papez circuit structures [2], and grid cells in entorhinal cortex [3]. In contrast, the neural systems supporting spatial navigation in humans are less well understood.

Neuroimaging studies of human navigation most commonly activate the posterior parahippocampal and retrosplenial cortices [4–10], regions that also respond strongly during passive viewing of navigationally-relevant visual stimuli such as scenes and buildings [11–14]. Consistent with these findings, damage to these areas often leads to wayfinding deficits [15]. These results suggest that parahippocampal and retrosplenial cortices are key nodes of the neuronal network that support spatial navigation in humans. But what are the specific functions of each of these nodes? In particular, what kind of navigationally-relevant information processing does each region support? Answering these questions is critical if we are to understand how spatial navigation is mediated by the human brain. Previous reviews of spatial navigation have either focused on other brain regions [16–18] or have restricted themselves the neuropsychological data [15]. Here I will focus specifically on the parahippocampal and retrosplenial cortices, reviewing recent results from neuroimaging,

neuropsychology, neuroanatomy and neurophysiology that illuminate the critical role that these regions play in human spatial navigation.

## The Parahippocampal Place Area (PPA)

### Basic Properties

In 1998, Kanwisher and I reported that a region of posterior parahippocampal cortex that we labeled the “parahippocampal place area” (PPA) responds preferentially to pictures of places [11]. In particular, the PPA responds strongly to complex visual scenes such as landscapes or cityscapes, weakly to nonscene objects (e.g. appliances, animals, vehicles) and to scrambled images, and not at all to faces [19]. The scene-preferential response in the PPA extends to a wide variety of scenes, including landscapes, cityscapes, rooms, tabletop scenes [20] and even “scenes” made out of Lego blocks [21]. Although the PPA is sometimes referred to as a “building” or “house” area [13,14,22], its response to buildings is smaller than the response to scenes [11] and this response is further reduced when subjects are induced to treat a building as a discrete object rather than as a partial scene [21], suggesting that scenes rather than buildings are the optimal stimulus.

PPA response to real-world scenes is only weakly affected by familiarity with the locations depicted in the scenes [21,23]. This suggests that the PPA is primarily involved in perception or encoding of the local scene, rather than higher-level mnemonic or navigational tasks [24]. However, it is important to note that a scene does not have to be visible for the PPA to respond. Like many high-level visual areas, the PPA activates during mental imagery, specifically of places [25], which may account for PPA activity during mental navigation tasks [5–7]. Furthermore, PPA response to nonscene objects can be modulated by the navigational or contextual significance of the stimulus [26,27]. Thus, the PPA appears to respond not just when scenes are visible, but also when scenes are cued or brought to mind.

The monkey homologue of the PPA is unclear. Although we have previously speculated that PPA is equivalent to the two cytoarchitecturally-defined regions (TF and TH) that comprise macaque parahippocampal cortex [28], a recent report by Saleem and colleagues [29] suggest that it might make up only a subset of this larger parahippocampal region. These authors identified a subregion of posterior TF, which they label TFO, that contains a prominent layer IV, making it more functionally similar to adjoining visually-responsive regions such as V4 and TEO than to the more anterior parts of parahippocampal cortex. The remainder of TF/TH may play a more general role in spatial memory (Box 1).

### BOX 1

#### Anterior Parahippocampal Cortex

Should the PPA be considered a single unit? There is some tantalizing yet inconclusive evidence for a functional division of labor between anterior parahippocampal cortex (PHC) and the posterior portion of the PPA (which extends into the lingual gyrus). In particular, anterior PHC may do more than just scene recognition; it might also play a more general role in spatial memory encoding [94]. This hypothesis rests on three lines of evidence. (Note that anterior PHC should not be confused with the anterior portion of the parahippocampal gyrus, which includes perirhinal cortex.)

1. Anatomical and connectivity data suggest that macaque region TFO can be distinguished from more anterior regions TF and TH. While TFO appears to be a visually-responsive region with a prominent layer IV, TF/TH may be more involved in spatial memory, combining inputs from both the ventral stream (V4, TE/TEO) and dorsal stream (retrosplenial, posterior parietal) before sending

outputs to entorhinal cortex and the hippocampus [63,95]. The connectivity between parietal cortex and anterior parahippocampal regions is strong enough that damage to the latter can lead to visuospatial neglect [96].

2. The neuropsychological literature points to a distinction between patients who have difficulties primarily in new environments [34–36] and others who have difficulties in both new and familiar environments [32–35,37]. Aguirre and D’Esposito [15] label the former syndrome *anterograde disorientation* and the latter *landmark agnosia*, although they note that it is unclear whether these syndromes are entirely distinct. Anterograde disorientation may be caused by damage to a topographical learning mechanism in the anterior PHC, while landmark agnosia may occur when more posterior scene recognition mechanisms are damaged [34].
3. Parahippocampal cortex is sometimes excised to treat intractable epilepsy. These patients typically have damage restricted to the anterior portions of the medial temporal lobe including anterior PHC, leaving undamaged the more posterior regions which are typically impacted in stroke patients. These epilepsy patients can exhibit problems on spatial memory tasks even when these tasks do not involve scene perception in any obvious way [97–99]. For example, Ploner and colleagues [100] found that patients with right parahippocampal lesions were impaired in their ability to remember locations in the left visual hemifield and make saccades to those locations after delays of 30s.

### Neuropsychological Studies

The parahippocampal/lingual territory encompassing the PPA is often damaged in posterior cerebral artery strokes, leading to problems with wayfinding [30], particularly when the damage is in the right hemisphere. Typically, these patients report that they cannot identify large topographical entities such as streets, buildings, or intersections, although they can determine the general semantic class to which these entities belong [31]. Sometimes they will compensate for this impairment by focusing on small details (e.g. a mailbox or a street sign) [32]. Their understanding of the spatial relationships between different locations is often preserved; thus, they can draw maps of the route they would take between different locations even though they cannot actually implement these routes in the real world [33,34]. Although at first glance their visual perception is unimpaired (with the common exception of a visual field cut), these patients often complain that some global organizing aspect of the scene is missing [35–37].

Mendez and Chierri [33] examined a typical patient (GN), whose wayfinding was impaired in both familiar and unfamiliar environments. GN had particular difficulties in nondescript environments such as corridors, public bathrooms, and theaters, reporting for example that “things look so similar in bathrooms; they all look all white.” When asked to identify prominent landmarks (e.g. buildings) and scenes (e.g. intersections) along a route, landmark recognition was normal, but his ability to identify scenes that did not contain a single prominent object-like landmark was severely impaired (Fig. 2a). Interestingly, if he was able to recognize a landmark or scene, he knew which direction to go from the landmark; indeed, he reported that he retained the equivalent of a “street guide” of his hometown in his head. In sum, he was unable to recognize scenes as wholes, but was able to use his apparently undamaged object-recognition system to identify landmarks. The fact that his scene analysis problem was exacerbated in relatively featureless environments such as bathrooms may indicate that he has particular difficulties when scenes must be parsed solely on the basis of spatial geometry.

My colleagues and I observed similar deficits in two patients with parahippocampal damage, one of whom we were able to verify had no functioning PPA [36]. Like GN, our patients found it exceedingly difficult to learn the topographical structure of new environments, presumably because of their inability to encode the local scene. In contrast, anecdotal evidence suggested that their spatial knowledge of pre-morbidly learned environments was more or less intact.

An interesting contrast to GN is provided by DF, a patient whose PPA is preserved but whose object form processing pathway is almost completely obliterated [38]. Despite her inability to recognize objects, DF was able to classify scenes in terms of general categories such as city, beach, or forest; furthermore, her PPA was activated when she performed these tasks. Taken together, GN and DF demonstrate a double dissociation between scene and object processing: the PPA appears to be part of a distinct processing stream for scenes that bypasses the more commonly studied object processing pathway [39].

### Information processing in the PPA

The data presented thus far indicate that the PPA is critical for identification of visual scenes but do not indicate the specific representations used to mediate this function. For any visual recognition mechanism, we can ask two fundamental information-processing questions. First, what is the spatial reference frame that the mechanism uses to represent the recognized entity? Here the answer seems to be that the PPA encodes scenes in an observer-centered (viewpoint-specific) rather than a world-centered (viewpoint-invariant) reference frame (see Box 2). Second, what are the basic elements that the system uses to represent the entity? Here the evidence suggests that the PPA doesn't encode every aspect of the scene; rather, it primarily encodes the spatial layout of the scene as defined by large fixed surfaces (Fig. 2b). In other words, the PPA treats the entire scene as a unified object, distinct from its component elements, which can be encoded and recognized in its own right. This contrasts with the hippocampus, which appears to encode a qualitatively different representation of the scene which includes information about specific objects and where they are located in space [40–44].)

#### BOX 2

##### Viewpoint- and position-specificity of scene processing in the PPA

There are at least two coordinate frames that the PPA could potentially use for scene encoding: viewer-centered or scene-centered. In the former case, the PPA would separately encode different views of a given scene, whereas in the latter case a single representation would be encoded that could be accessed from different vantage points. My colleagues and I addressed this issue in a series of experiments by exploiting a phenomenon known as fMRI repetition suppression (fMRI-RS), which is the reduction of fMRI response obtained when stimuli are presented more than once. The key question was whether repeating a scene from a different viewpoint leads to a reduced response; if so, the two views of the scene must be (to some extent) representationally equivalent. We consistently observed fMRI-RS for same-viewpoint repetitions but not for different-viewpoint repetitions, arguing for viewpoint-specific processing [20,23,101,102]. Interestingly, some cross-viewpoint adaptation was observed when stimuli were repeated over longer time intervals [23,101,102] or when the viewpoint changes were part of an ordered sequence reflecting coherent motion around the scene [21,103]. However, even in these cases, complete viewpoint-invariance was never achieved.

A second basic question about any visual representation is the degree to which it is sensitive to the position of the stimulus on the retina. MacEvoy and I [104] found that RS effects in the PPA were insensitive to cross-midline changes in retinal position of up to

12 degrees, an amount of visual change to which object-selective regions such as the lateral occipital complex (LOC) were highly sensitive. These results suggest receptive fields in the PPA are larger than those in object-processing regions, which may reflect PPA involvement in the encoding of large, extended scene features such as walls or hillsides.

Taken together, the results of the viewpoint-invariance and position-invariance studies suggest that the PPA is sensitive to visual changes induced by movement of the observer around the scene (i.e. viewpoint changes), but insensitive to visual changes induced by eye movements (i.e. retinal position changes), which are less navigationally relevant. Similar results have been observed in RSC; however, this region appears to be somewhat less sensitive to specific perceptual details such as viewpoint [23] or scene framing [105]. Interestingly, despite neurophysiological and neuropsychological evidence for viewpoint-invariant place representations in the hippocampus [41,106], my colleagues and I have not observed consistent evidence for viewpoint-invariant fMRI adaptation in this region. This may simply reflect the fact that fMRI-RS effects in the hippocampus are somewhat recalcitrant (e.g. [107,108], but see [109]) perhaps because neurons in this region have different inherent properties than those in neocortex. Alternatively, fMRI-RS in the hippocampus may depend more on explicit memory judgments that are shaped by task requirements than on stimulus repetition per se [110]. In particular, the extent to which the hippocampus considers two views of the same scene to be “the same” or “different” may depend on whether the task is to judge place repetitions or view repetitions (c.f. [111]), in contrast to the PPA where fMRI-RS is driven by view repetition irrespective of task [112].

Supporting the spatial layout hypothesis is the fact that the PPA response to indoor scenes does not depend on the presence of discrete objects within the scene. The PPA responds equally strongly to empty rooms and rooms filled with furniture and objects, while its response to arrays of objects drawn from the rooms but displayed on a blank background is quite weak ([11]; Fig. 2c). Thus, the PPA appears to be driven primarily by fixed background elements such as walls which define the geometry of local space rather than by smaller objects within that space. (However, see [26] for an alternative view.) Subsequent studies have reported that the PPA responds more strongly to “scenes” made out of Lego blocks than to “objects” made out of the same materials ([21,36]; Fig. 2c), more strongly to full scenes (e.g. a kitchen) than close-up scenes (e.g. a close-up of the stove) or to scene-diagnostic objects (e.g. the stove with all background information removed) [45], and more strongly to scenes that retain their spatial organization than to scenes whose surfaces have been rearranged so that they no longer define a coherent 3-dimensional space [11]. These results indicate that PPA response is strongest to stimuli that provide the most information about the geometric structure of local space, even when other aspects of the stimuli are tightly controlled.

Although these results are consistent with the idea that the PPA encodes “spatial layout”, there are many different varieties of spatial layout that might be encoded. One possibility is that the PPA encodes the geometry of the fixed elements of scene as ascertained from a particular point of view. For example, the PPA might encode a kind of “shrink-wrapped” geometry of the scene akin to its surface shape, or a rough representation of the major barriers and affordances within the scene. Alternatively, the PPA might be less concerned with encoding the scene itself than with processing the observer’s location and orientation relative to it [20], perhaps by first extracting information about the principal axes of the observed space. Some evidence for this last idea comes from a recent study that found that PPA activity during a learning episode did not depend strongly on the stimulus materials

(ground-level vs. aerial views of a scene) but did depend strongly on whether or not the observer had to keep track of a changing orientation relative to the scene [46].

Finally, an important unresolved issue is whether the PPA solely encodes geometric information, or whether it also encodes information about the distribution of visual features such as colors or textures within a scene [47]. The idea that the PPA encodes only geometry fits nicely with behavior studies indicating that animals and humans preferentially use the shape of local space to reorient when lost [48]. Indeed, ecological arguments suggest that fixed topographical elements such as walls, hillsides, or pathways should be particularly important for place recognition, as these are the aspects of a place that tend to be unchanging over time [49]. However, some recent evidence suggests that lingual/fusiform regions abutting the PPA are sensitive to material properties of objects such as color or texture [50], a finding that argues against purely geometric encoding in the PPA. One possibility is that different subregions within the PPA encode the geometric and nongeometric properties of the scene; however, at this point this idea is purely speculative.

## The Retrosplenial Complex (RSC)

### Basic Properties

A second focus of cortical activity during navigation tasks is found in the retrosplenial cortex/posterior cingulate/medial parietal region, near to the point where the calcarine sulcus joins the parietal-occipital sulcus. Retrosplenial cortex (BA 29 and 30) adjoins and is partially encircled by the posterior cingulate (BA 23 and 31) [51–56]; consequently, these labels are often used somewhat interchangeably when describing the locations of functional activations. Because of these ambiguities, I use the term retrosplenial complex (RSC) to refer to this functional-defined scene-responsive region, which is not necessarily identical to the anatomically-defined retrosplenial cortex [26].

RSC is strongly active during scene viewing, scene imagery [25], and mental imagination of navigation through familiar environments [8]. In contrast to the PPA, where place familiarity effects are usually quite small, RSC responds 50% more strongly to familiar than to unfamiliar places [23,57], suggesting that RSC is involved in recovery of long-term spatial knowledge about familiar environments. Further evidence for this idea comes from recent studies that reported that RSC activity was significantly greater when subjects reported the location of a campus scene than when they simply reported whether it was familiar or not ([24]; Fig 3a) and that RSC activity during learning of a virtual reality town corresponded to the total amount of survey knowledge acquired ([58], Fig. 3b; see also [59] for similar results in mice.) Although RSC has often been described as being part of a “default network” because it tends to deactivate during a variety of cognitive tasks [60], its response to scenes is significantly above baseline, reflecting true involvement in scene processing rather than simply an absence of disengagement for these stimuli (Fig. 1).

Anatomical connectivity data are also consistent with the idea that RSC supports spatial memory. In the monkey, the retrosplenial/posterior cingulate region is strongly interconnected with parietal lobe regions 7a and LIP, as well as medial temporal regions such as entorhinal cortex, pre-subiculum/post subiculum, and parahippocampal regions TF/TH [52,61–63]. Thus, RSC is well-positioned to translate between egocentric spatial codes in the parietal lobe and allocentric spatial codes in the medial temporal lobes [64,65]. Projections from the anterior thalamus [55,66] and dorsolateral prefrontal cortex [52,55] might provide critical head direction and working memory inputs which help mediate this translation [67]. Similar anatomical connectivities are found in rats [68,69].

## Neuropsychological Data

Navigational difficulties are frequently reported when the retrosplenial region is damaged by stroke in humans [70–77], or lesioned in rats [78]. Often, the onset of the impairment is quite dramatic. For example, one patient suddenly became lost while returning home from work: “He could recognize buildings and the landscape and therefore understand where he was, but the landmarks that he recognized did not provoke directional information about any other places with respect to those landmarks. Consequently, he could not determine which direction to proceed.” [71] Such navigational difficulties have been reported after lesions affecting the right hemisphere [70,72,74,75], left hemisphere [71,75,77], both hemispheres [76], and retrosplenial white matter [73]. Interestingly, these problems often clear up after a few months with unilateral damage [70,75] but not bilateral damage [76], possibly because the undamaged hemisphere begins to compensate [8].

In contrast to parahippocampally-damaged patients, retrosplenially-damaged patients report that they can identify scenes, but they cannot use them for purposes of orientation. Because of this deficit, these patients are unable to find their way, even in quite familiar environments. When asked to draw or label maps of their neighborhood or floor plans of their house, most are unable to do so [70,71,73,76,77] (but see [74]). A few can verbally recount the routes that they cannot successfully implement [74,75], but most cannot [70,71,73,76,77]. Although they can sometimes describe what one would expect to see from a particular vantage point [72,74] they cannot determine the spatial relationship between two locations if one cannot be seen from the other [70].

As might be expected given the anatomical connectivities of the region, a key element of the retrosplenial syndrome appears to be an inability to translate between egocentric/viewpoint-dependent and allocentric/survey-level representations. For example, one patient was completely unable to use a map to indicate her viewpoint relative to her house [74] (Fig. 3c), while another could not identify her current position within a room by pointing to a floor plan or a miniature model of the room [72]. Others could not follow a route within a room if this required them to make changes in orientation [8] [73]. This inability to convert back and forth between egocentric and allocentric representations might severely impact navigation by making it impossible to relate the local scene to an allocentric spatial representation such as a cognitive map.

## Information processing in RSC

Although the above results indicate that RSC supports mechanisms that allow us to situate ourselves in global space, little is known about the specific representations that the RSC uses to mediate these mechanisms. Rodent neurophysiological studies indicate that RSC neurons can encode a variety of spatial quantities, such as head direction (HD cells; [79]) and head direction whilst in a particular location (Direction-dependent place cells [80]). However, it is currently unclear whether these different varieties of cells are found within the same region, or distinct medial parietal/posterior cingulate subregions. Nor is it clear whether these cell types are found in human RSC as defined by functional imaging studies.

Keeping these caveats in mind, I can offer some speculations about information processing in RSC during navigation. In a recent neurophysiological study, Sato and colleagues recorded from medial parietal neurons (i.e. possibly RSC) while monkeys followed well-learned paths through a multi-room virtual reality environment [81]. Of the many neurons that responded strongly during this task, 77% responded specifically when the animal made a particular action (turn left, right, or move forward) at a particular location. One possible interpretation of these results is that the neurons encoded the bearings from each location to the next point in the path. Sato and colleagues did not attempt to distinguish between

egocentric and allocentric bearings (“turn to the left” vs. “turn to the east”); however, results from delayed-saccade experiments indicate that neurons in this region encode target locations in both coordinate frames [82]. Interestingly, many of the neurons in Sato’s study responded in a path-selective manner, suggesting that, at least during the initial stages of learning an environment, RSC distinguishes between paths even when they pass through the same location.

These results are consistent with the idea that RSC supports representations that allow “you are here” information to be translated into “your goal is to the left” (as well as the opposite, egocentric-to-allocentric translation), an idea that draws additional support from the neuropsychological data indicating that RSC patients cannot determine the direction to unseen goals. In a recent report, Byrne et al. propose a computational model of how this transformation might be performed, in which RSC uses heading direction inputs from the thalamus to compensate for the rotational offset between the egocentric and allocentric coordinate frames [67]. In addition, one might hypothesize that RSC is more than just a device for translating between hippocampal and parietal spatial codes, it might also encode its own representation of the spatial structure of familiar environments which might be sufficient to support some kinds of navigation when the hippocampus is damaged [83,84] or in simple and/or very familiar environments [85]. Specifically, by encoding routes or bearings between prominent locations, RSC might support a topological graph [86,87] that supplements the more metrical and detailed cognitive map supported by the hippocampus and entorhinal cortex [17,88].

### **Conclusion: Two Processing Streams for Visually-Guided Navigation?**

The PPA and RSC appear to play distinct but complementary roles during spatial navigation. The PPA encodes a representation of the local scene that allows it to be remembered and subsequently recognized, while RSC supports mechanisms that allow one to orient oneself within the broader spatial environment and to direct one’s movement towards navigational targets that are not currently visible. Interestingly, this division concords well with recent results from cognitive psychology, which indicate that spatial coding can use two different kinds of representation: viewpoint-specific scene snapshots, and world-centered representations of spatial locations [89]. Since both PPA and RSC respond strongly during passive observation of navigationally-relevant visual stimuli (i.e. scenes), these regions might be conceptualized as supporting distinct processing streams for visually-guided navigation, both of which provide critical inputs to the entorhinal cortex and the hippocampus.

Although speculative, I hypothesize that these two input streams might be optimized for two different navigational situations. When we are lost and need to re-establish our general location, scene recognition mechanisms in the PPA are likely to be critical, potentially allowing the correct “map” to be selected in the hippocampus. Furthermore, when traveling through an unfamiliar environment, scene representations in the PPA might provide the building blocks out of which a larger topographical representation can be formed. Orientation mechanisms in RSC, on the other hand, might come into play once we know approximately where we are, by allowing us to specify directions to navigational goals [67]. These two processing streams would work in concert with a number of other neural mechanisms not described here, such as path integration mechanisms [90–92], and mechanisms for establishing head direction by reference to distal landmarks [2,93]. Future studies should relate these mechanisms more closely to spatial codes delineated by cognitive psychology and explore how they might support both spatial and nonspatial memory.

**BOX 3****Outstanding Questions**

- What is “spatial layout” and how might it be encoded at the neural level? In particular, do neurons in the PPA respond selectively to different visual features (textures, colors), different environmental shapes (e.g. opening to the left/barrier to the right vs. barrier to the left/opening to the right), or different spatial relationships between the observer and the environment (e.g. current heading is a 30 degree offset from the principal axis of the local environment)?
- Janzen and colleagues [27] report that a posterior parahippocampal region corresponding to the PPA responds more strongly to objects that were previously encountered at intersections than to equivalent objects that were previously encountered in non-navigationally-relevant positions. What accounts for this “landmark object” effect? Does it indicate that the PPA encodes the appearance of the landmark objects, the locations of the objects, or the local spatial framework associated with each object?
- The location and boundaries of the PPA are well-described in the literature, but RSC is comparatively less studied. Does RSC operate as a unified functional unit, or is an agglomeration of more anatomically restricted components? If the former, what are its anatomical boundaries? If the latter, what are the distinct functions of the RSC subcomponents (retrosplenial cortex, posterior cingulate, and parietal occipital sulcus)?
- Retrosplenial activity is often observed during episodic and autobiographical memory tasks that do not have an obviously spatial component [113]. Does this indicate episodic/autobiographical memory includes an intrinsic spatial component, such as “scene construction” [114]? Or does this indicate that the “true” function of RSC should be described in more general terms that could potentially include processing of both spatial and nonspatial information?
- Results from neuroimaging and animal lesion studies suggest that navigation along highly familiar routes involves different memory systems than navigation along a novel route [115]. In particular, planning a novel route appears to involve hippocampal spatial representations, while navigation along a “well-worn” route might utilize a response-based strategy that depends more on the basal ganglia (specifically, the caudate nucleus) [116,117]. Do the PPA and RSC play a role in response-based navigation? In particular, might the PPA encode critical landmarks that prompt people to “turn left” at a certain point? [118] And how might the information that it is important to “turn left here” be differently encoded in the caudate nucleus vs. RSC?

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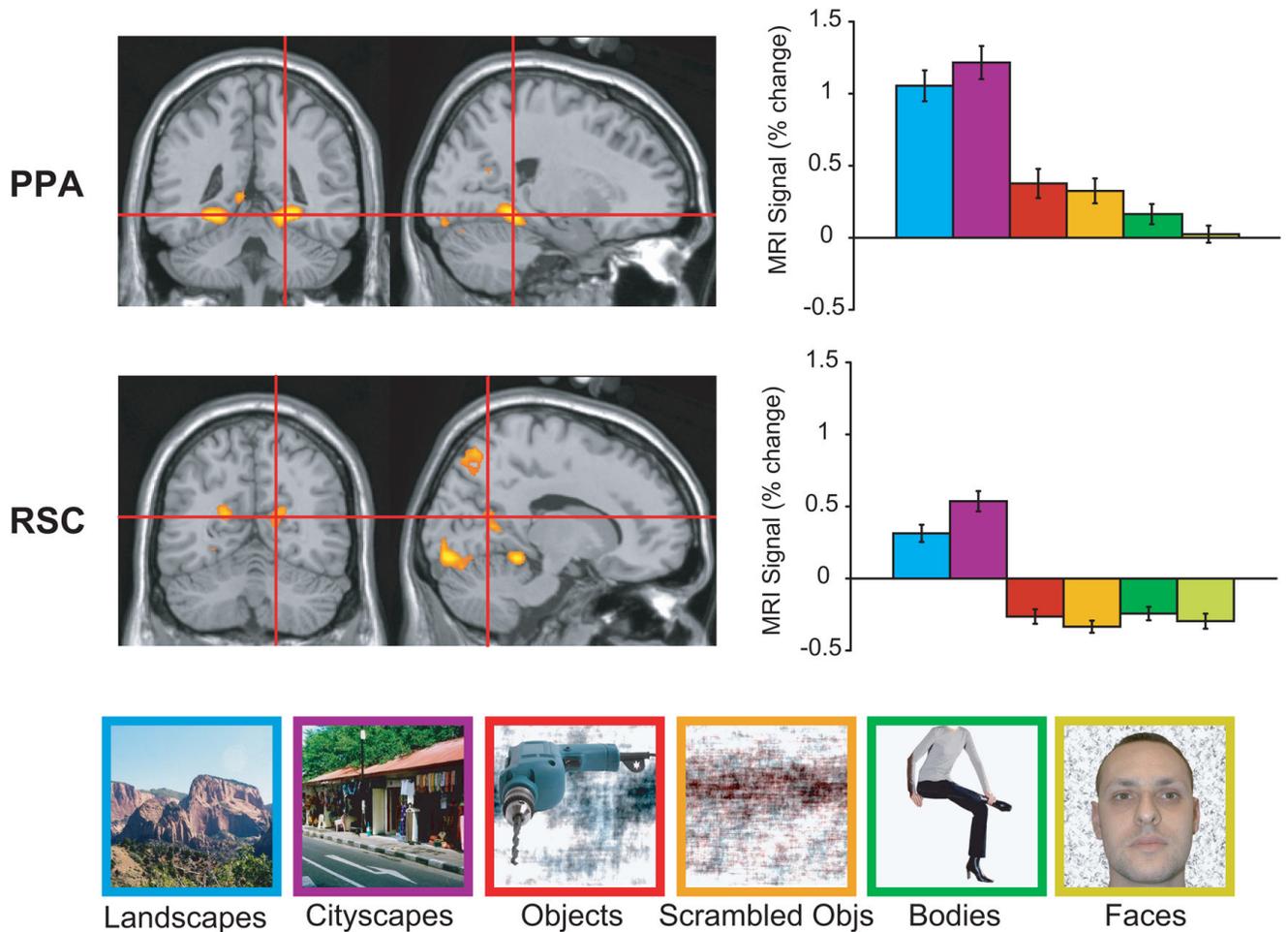
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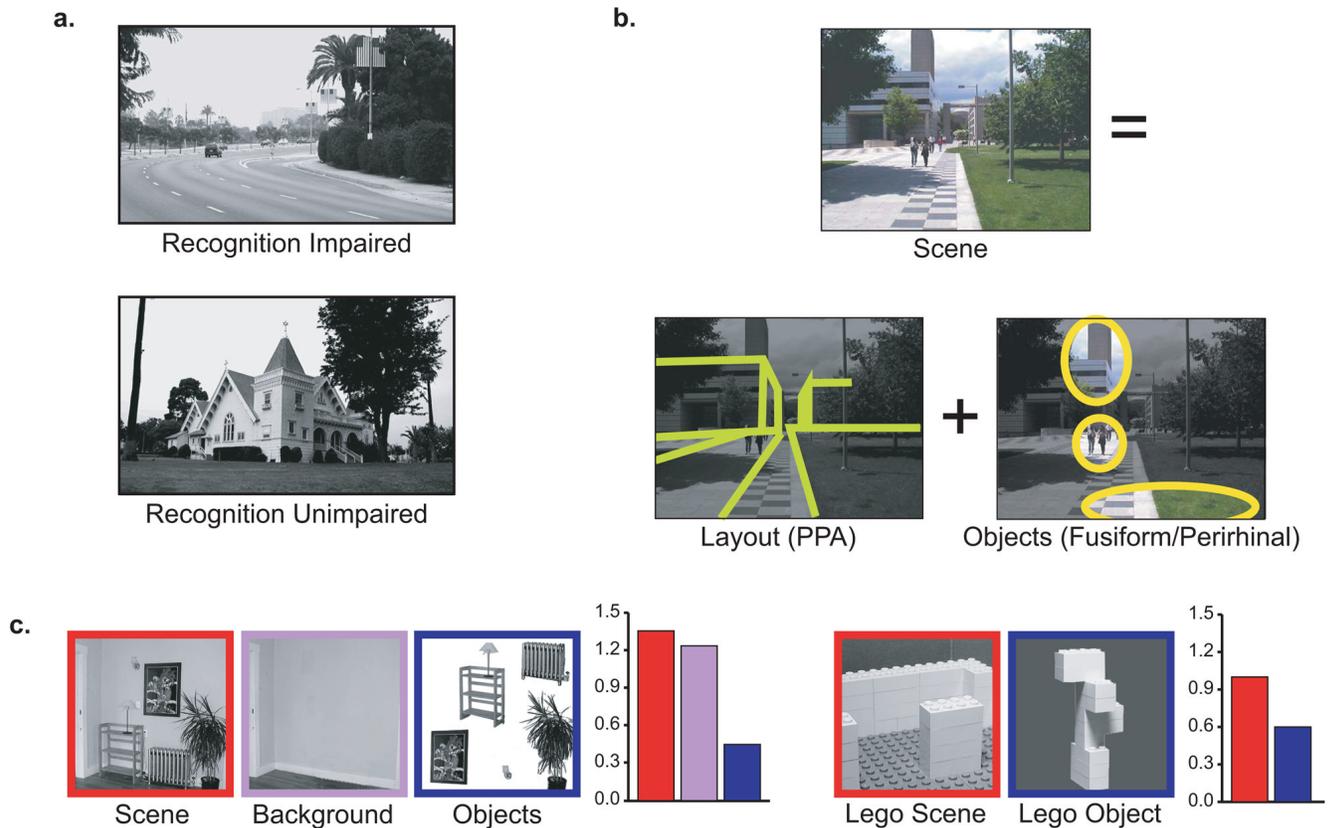
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**Fig 1. Location and basic response properties of the PPA and RSC**

Brain maps showing the PPA and RSC are plotted on a reference anatomical brain in standard space. Orange voxels responded more strongly ( $p < 0.05$ , corrected for multiple comparisons) to scenes than to nonscene objects in a random effects group analysis ( $N=38$ ; previously unpublished data). Crossbars indicate the location of the PPA and RSC. Bar charts show the response in the PPA and RSC to six stimulus categories, plotted as percent signal change relative to a fixation (no-stimulation) baseline. For this analysis, the PPA and RSC were functionally defined on each subject as described previously (e.g. [102]). PPA clearly responds most strongly to scenes, although it is not completely unresponsive to other stimuli. RSC response is significantly above baseline for scenes, but significantly below baseline for other stimuli.

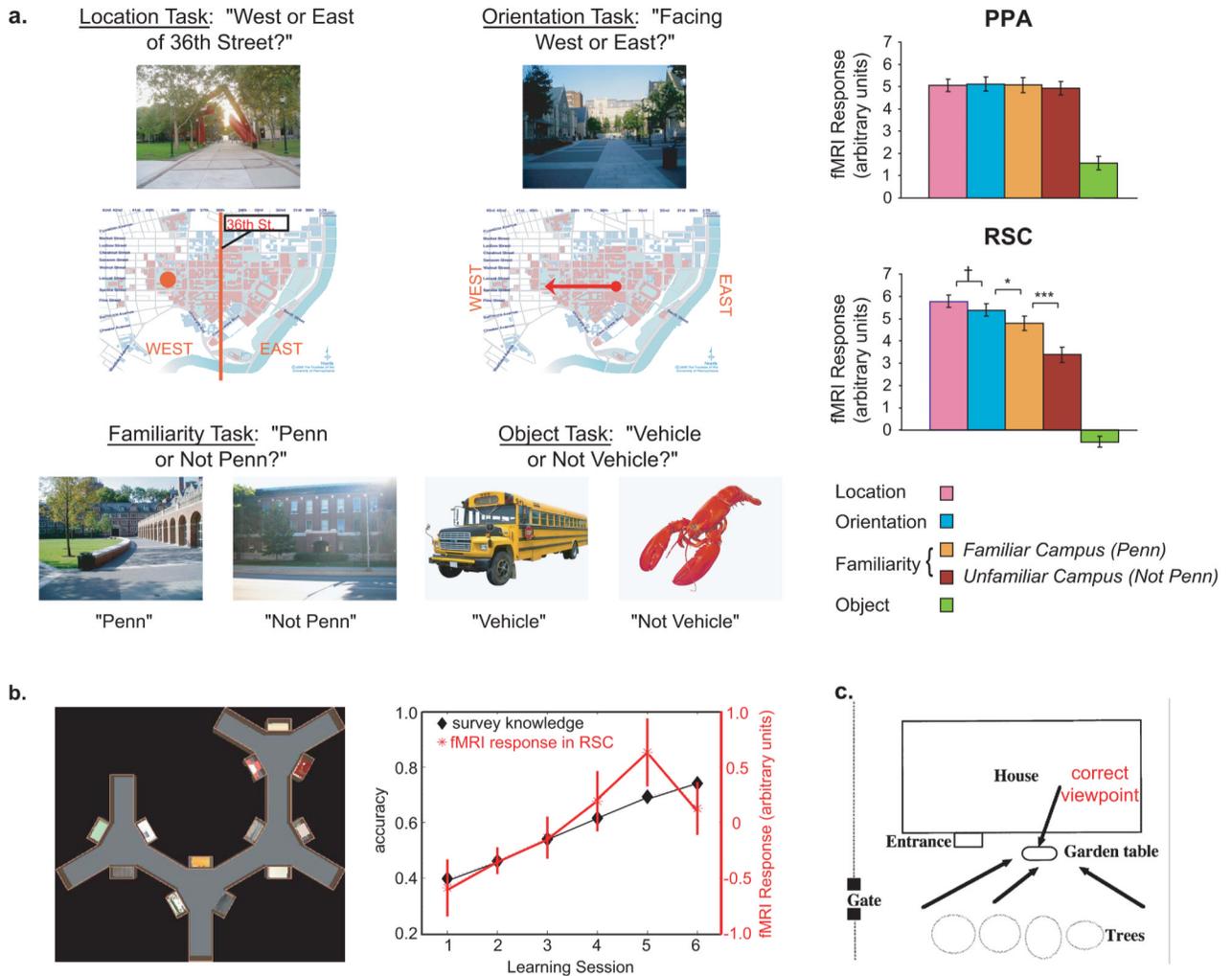


**Fig. 2. The Parahippocampal Place Area and scene encoding**

a. Neuropsychological evidence for PPA involvement in scene recognition. A patient with right hemisphere parahippocampal damage was unable to recognize scenes unless they contained a single prominent object-like landmark, suggesting that patients with PPA damage can recognize large objects but not scenes per se [33].

b. Under the spatial layout hypothesis, the PPA encodes the overall spatial layout of the scene as defined by fixed topological features, while information about the individual objects in the scene is encoded in the lateral occipital complex, fusiform gyrus, and perirhinal cortex. When the PPA is damaged, patients report that they can see the objects in the scene but the overall organization of the scene is lost, suggesting that normal scene perception involves the integration of object and layout information.

c. The PPA responds strongly to layout-defining scene features such as walls and ground planes. In particular, the PPA response to indoor scenes is not significantly changed by removing the objects, but is significantly reduced by removing the background [11]. Furthermore, PPA response to the Lego “scenes” is significantly greater than response to Lego “objects” [21].



**Fig 3. RSC supports retrieval of long-term spatial knowledge**

a. RSC activity corresponds to retrieval of long-term spatial knowledge. University of Pennsylvania students were scanned with fMRI while viewing photographs of their home campus (Penn), an unfamiliar campus, or nonscene objects [24]. For the home campus photographs, they either retrieved spatial information (location or orientation) about each scene or made a simple familiarity judgment. RSC response was stronger during location or orientation judgments than during familiarity judgments. Furthermore, RSC response was higher when viewing images of the familiar campus than when viewing images of the unfamiliar campus, even when task was controlled. These results demonstrate that RSC response is stronger when viewing scenes whose spatial surroundings are known (Penn Images) than when viewing scenes whose spatial surroundings are unknown (Not Penn Images) and is even further enhanced when subjects explicitly retrieve long-term spatial knowledge (e.g. location, orientation). Note that PPA response was unaffected by task or familiarity, consistent with its proposed role in local scene perception. (Significance symbols: † $p < 0.06$ , \* $p < 0.05$ , \*\*\* $p < 0.001$ ).

b. RSC activity during learning of a virtual-reality town increases in tandem with subjects' increasing survey knowledge about the town [58].

c. RSC damage leads to an inability to understand the relationship between egocentric and allocentric representations. Here one such patients was shown a photograph of the garden of

her house, and was asked to determine the viewpoint from which the photograph was taken [74]. Her responses are indicated by arrows; the correct response is also noted. She was unable to perform this task accurately.