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The Parahippocampal Place Area: Recognition, Navigation, or Encoding?

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Summary

The parahippocampal place area (PPA) has been demonstrated to respond more strongly in fMRI to scenes depicting places than to other kinds of visual stimuli. Here, we test several hypotheses about the function of the PPA. We find that PPA activity (1) is not affected by the subjects' familiarity with the place depicted, (2) does not increase when subjects experience a sense of motion through the scene, and (3) is greater when viewing novel versus repeated scenes but not novel versus repeated faces. Thus, we find no evidence that the PPA is involved in matching perceptual information to stored representations in memory, in planning routes, or in monitoring locomotion through the local or distal environment but some evidence that it is involved in encoding new perceptual information about the appearance and layout of scenes.

Introduction

The medial temporal lobes of the human brain are believed to play a key role in both memory (Squire and Zola-Morgan, 1991) and navigation (O'Keefe and Nadel, 1978; Aguirre et al., 1996; Maguire et al., 1996; Ghaem et al., 1997). However, the precise way in which this region mediates these different functions is currently unknown. Consequently, the identification of functionally distinct subregions within the medial temporal lobes is of considerable interest (Martin et al., 1997). In an earlier paper (Epstein and Kanwisher, 1998), we reported the existence of a region within human parahippocampal cortex that was significantly more active when subjects viewed complex scenes such as rooms, landscapes, and city streets than when they viewed photographs of objects, faces, houses, or other kinds of visual stimuli. This activity did not depend on the presence of discrete objects within the scene but did depend on whether the surfaces in the scene defined a coherent space. We named this region the "parahippocampal place area," or PPA, because it responded strongly whenever subjects viewed an image of a place.

These results implicated the PPA in the processing of information about the layout of local space. However, they did not allow us to determine the specific function of the PPA. In this paper, we present four experiments designed to examine this issue. Broadly, we will consider three possibilities: the PPA may be involved in (1) place recognition, (2) route planning through either the immediate or the distal environment, and (3) perceptual or mnemonic encoding. By "involvement" we mean merely that the PPA is selectively engaged when a given task is being carried out. (As in all imaging studies, answering the question of whether that area carries out computations *necessary* for a task requires converging evidence from other methods such as patient studies.) Note that these three possible PPA functions are not mutually exclusive. We will now consider each in turn.

By place recognition, we mean the matching of current perceptual information to the memories of places that have been encountered in the past and stored in one's cognitive map (O'Keefe and Nadel, 1978). There are a number of cases in the neuropsychological literature of patients who have lost the ability to recognize places, despite retaining the ability to follow maps and understand the spatial relationships between different points (Whiteley and Warrington, 1978; Landis et al., 1986; Habib and Sirigu, 1987; McCarthy et al., 1996; reviewed by Aguirre et al., 1998a; Aguirre and D'Esposito, 1999). These patients are particularly impaired at recognizing large-scale environmental features (e.g., buildings, street scenes) and can often compensate for their deficit by using small details (e.g., a lamppost, the shape of a mailbox) as navigational cues. The region of damage in these cases of "landmark agnosia" often includes parahippocampal cortex (Habib and Sirigu, 1987; Aguirre et al., 1998a), which suggests that the PPA may be involved in place recognition. Although subjects in our previous experiments were not specifically instructed to identify the places depicted in the scenes, it is likely that they attempted to do so anyway. Here, we examine the role of the PPA in place recognition by comparing PPA response to places familiar to the subjects with its response to unfamiliar places they had never visited (Experiment 1) and by measuring its response to "scenes" made out of Lego blocks (Experiment 2). If the scene-selective activity observed in the PPA reflects the operation of a place recognition mechanism, then one might expect the PPA response to familiar and unfamiliar places to differ, and one would not expect the PPA to respond strongly to Lego scenes, which are not real places in the world.

A second possible PPA function is planning routes to destinations stored in one's cognitive map (Maguire et al., 1997, 1998). In order to accurately perform this task, one must first be able to determine one's current location in large-scale space—one cannot plan routes from places one does not know (O'Keefe and Nadel, 1978; Gallistel, 1990). Thus, if the PPA is a route planning mechanism, it should not be particularly active when viewing the unfamiliar places in Experiment 1 or the Lego scenes in Experiment 2. But even if the PPA does not play a role in planning routes to distant locations, it still may play a role in another navigational task: monitoring or guiding locomotion through the immediate (i.e.,

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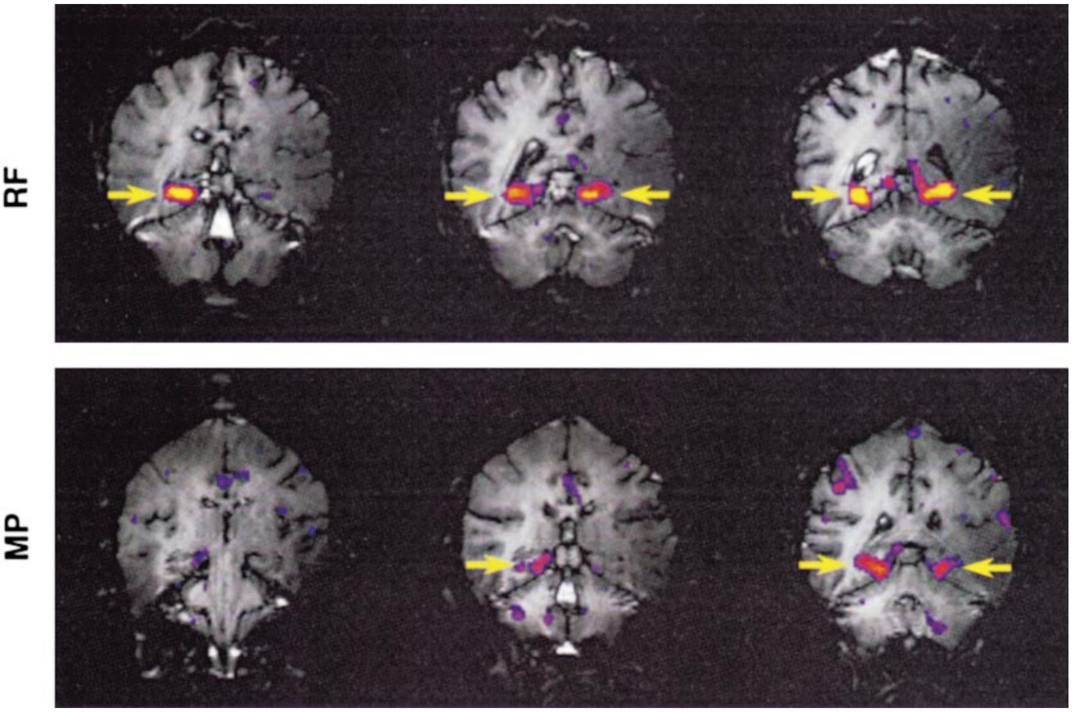


Figure 1. Anatomical Location of the PPA (Yellow Arrows)

Three adjacent slices from two subjects are shown. Functional data from Experiment 1 are overlaid on high-resolution T1-weighted anatomical images of the same slice. Right hemisphere is on the left, and images progress from anterior (left) to posterior (right). Significance levels reflect the results of a Kolmogorov-Smirnov test comparing the MR signal intensity during viewing of scenes to signal intensity during viewing of faces and objects. The response properties of the coil used precluded our obtaining Talaraich coordinates for the PPA in this experiment. However, the coordinates of the PPA averaged over four subjects in an earlier experiment (Epstein and Kanwisher, 1998, Experiment 1) were 20, −39, −5 (M–L, A–P, S–I) in the right hemisphere and −28, −39, −6 in the left hemisphere.

currently visible) environment. In other words, the PPA may be less involved in accessing one's cognitive map to figure out how to get from here to the other side of town than in analyzing the current scene to figure out how to get from here to the other side of the street. We test this hypothesis in Experiment 3 by comparing PPA response to individual snapshots with its response to a "movie" sequence consisting of a temporally ordered series of photographs taken from a camera moving through a fixed scene. If the PPA is involved in monitoring or guiding locomotion through the local environment, then we might expect to see a higher response in the movie condition, because subjects have the impression that they are actually going somewhere.

Finally, the PPA might be involved in either perceptual or mnemonic encoding. Supporting this possibility is the fact that some patients with topographical disorientation have particular difficulty in *new* environments (Ross, 1980; Habib and Sirigu, 1987). Furthermore, regions within parahippocampal cortex have been observed that respond more to novel than repeated stimuli (Stern et al., 1996; Gabrieli et al., 1997) and more to subsequently remembered than subsequently forgotten stimuli (Brewer et al., 1998; Wagner et al., 1998). The location of these putative encoding regions has not been compared directly with the PPA, but their proximity to the PPA suggests that the latter may play a critical role in encoding novel place information. We tested this hypothesis in Experiment 4 by comparing PPA response to novel scenes with its response to scenes that have been viewed many times. If the PPA is involved in encoding, we would expect greater response to novel scenes.

In all four experiments, the PPA was functionally defined for each subject using data from a separate set of scans from the same scan session (see Experimental Procedures). The PPA was defined as the set of all contiguous voxels within the parahippocampal region that responded significantly more during viewing of scenes than during viewing of faces or objects. As in our previous report, we found that the PPA could be localized in a highly consistent anatomical location in all subjects tested (see Figure 1).

Results

Experiment 1

Experiment 1 tested the hypothesis that the PPA is involved in place recognition, by testing whether it responds differently to images of familiar and unfamiliar places. While being scanned with functional magnetic resonance imaging (fMRI), subjects viewed photographs of (1) scenes from a familiar environment (the campus of their own college); (2) scenes from an unfamiliar environment (the campus of an unfamiliar college); (3) landmarks from a familiar environment (buildings from their own college); (4) landmarks from an unfamiliar environment (buildings from an unfamiliar college); (5) common, everyday objects; and (6) faces. All subjects reported

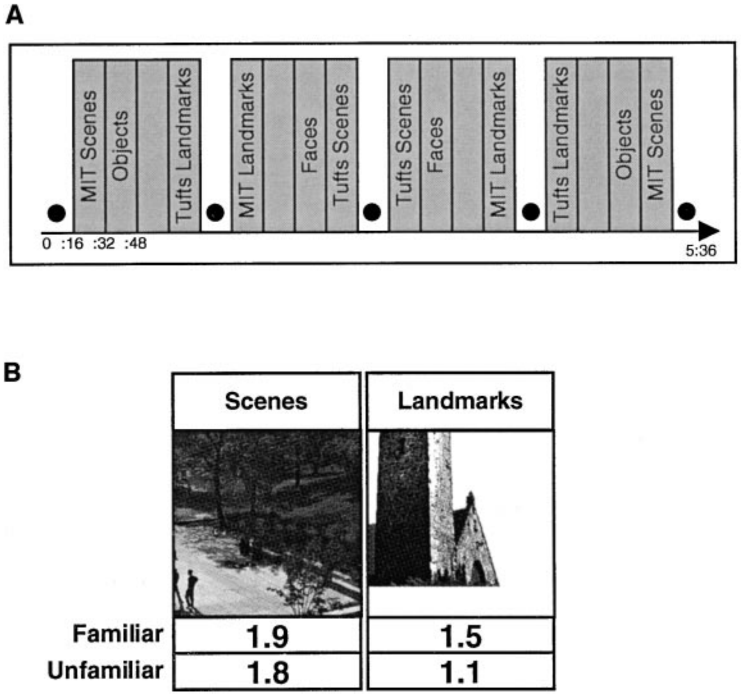


Figure 2. Design and Results of Experiment 1

(A) Series of conditions in a single scan. Each scan was 5 min and 36 s long and was divided into 16 epochs in which stimuli were presented and 5 fixation epochs (black dots). Within each stimulus epoch, subjects saw 20 different photographs of the same type. Each stimulus condition occurred twice within a scan. (During unlabeled epochs, subjects viewed stimuli designed to test hypotheses not discussed here.)

(B) Percent signal change (relative to a fixation baseline) within the PPA during viewing of familiar and unfamiliar scenes and landmarks, averaged over all subjects and scans. Familiar stimuli were MIT scenes and landmarks for MIT students, and Tufts scenes and landmarks for Tufts students, while unfamiliar stimuli were the opposite. Subjects also viewed objects and faces in this experiment; the average percent signal change within the PPA was 0.4% for objects and 0.0% for faces.

that they recognized most or all of the scenes and landmarks from their own college campus but none of the scenes or landmarks from the other campus.

Figure 2B and Table 1 show the average percent signal change (relative to a fixation baseline) within the PPA for all stimulus conditions. Values are averaged over all runs for all eight subjects. A three factor (scene/landmark × familiar/unfamiliar × passive/1-back) ANOVA on the critical stimulus conditions showed that the response in the PPA to full scenes was significantly higher than the response to individual landmarks ($t[7] = 2.9$, $p < 0.001$). In addition, there was a significant overall advantage for stimuli from the familiar environment ($t[7] = 3.3$, $p < 0.05$). Separate ANOVAs found that this familiarity advantage was significant only for the landmarks ($t[7] = 4.0$, $p < 0.01$) but not for the full scenes ($p > 0.15$). The interaction between familiarity/unfamiliarity and stimulus type fell short of significance overall ($F[1,7] = 3.6$, $p = 0.10$) but was significant during passive viewing runs ($F[1,7] = 7.7$, $p < 0.05$] (presumably because subjects have time to imagine the surroundings of familiar but not unfamiliar landmarks in this task; see Discussion). The failure to find a difference between familiar and unfamiliar scenes cannot be attributed to the fact that each scene was viewed many times over the course of the experiment, as post hoc analyses revealed there was no difference in response between familiar and unfamiliar scenes even in the very first epochs in which these pictures were viewed (average percent signal change: 2.2% for familiar scenes, 2.1% for unfamiliar scenes, $t < 1$ for the difference). In sum, Experiment 1 failed to find evidence that the PPA response to scenes was correlated with successful recognition of the place depicted.

The effect of task (passive viewing versus 1-back repetition detection) is shown in Table 1. Overall, there was no difference in performance between the two tasks ($t < 1$). However, there was a significant interaction between

Table 1. Average Percent Signal Change for Passive Viewing and 1-Back Repetition Detection Tasks in Experiments 1 and 2

Experiment 1	Familiar Scenes	Unfamiliar Scenes	Familiar Landmarks	Unfamiliar Landmarks	Objects	Faces	
1-back	2.0	1.8	1.4	1.1	0.5	0.0	
Passive	1.9	1.8	1.6	1.2	0.4	0.0	
Average	1.9 (0.7)	1.8 (0.4)	1.5 (0.4)	1.1 (0.3)	0.4 (0.1)	0.0 (0.1)	
Experiment 2	**Furnished Rooms**	**Empty Rooms**	**Legos with Animals**	**Legos without Animals**	**Lego Objects**	**Real Objects**	**Faces**
1-back	1.8	1.7	1.5	1.3	0.8	0.7	0.2
Passive	1.3	1.4	0.9	0.8	0.5	0.6	0.1
Average	1.6 (0.3)	1.6 (0.3)	1.2 (0.3)	1.0 (0.3)	0.6 (0.3)	0.6 (0.2)	0.0 (0.1)

Variances are in parentheses.

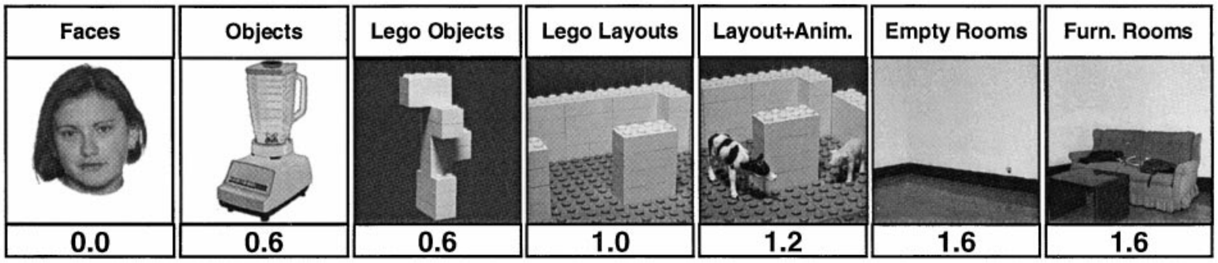


Figure 3. Example Stimuli and Results for Experiment 2, Showing the Average Percent Signal Change within the PPA for Each Stimulus Condition

task and picture type ($F[1,7] = 8.7$, $p < 0.05$), reflecting the fact that response to scenes was higher (compared to passive viewing) when subjects performed the 1-back task, but the response to landmarks was lower in the same task. Possible reasons for this pattern will be considered in the Discussion.

Experiment 2

The results of Experiment 1 demonstrated that PPA activity was not affected by the recognizability of the place depicted. But would spatial layout information be sufficient to drive the PPA, even in the absence of *any* plausible sense that one is looking at a place that might be in one's cognitive map? Experiment 2 tested this hypothesis by testing whether the PPA response to artificial "scenes" made out of Lego blocks (shown in Figure 3) would be higher than the response to objects made of the same Lego materials. The Lego scenes were designed to look like places, but were clearly not real places that the subjects could have ever visited. All subjects reported that the Lego scenes did indeed look like places while the Lego objects did not. There were two Lego layout conditions: one in which small toy animals were placed in the layouts to enhance the interpretability of the geometry of the scenes, and one in which bare Lego layouts were shown. Subjects also viewed photographs of furnished rooms, empty rooms, common objects, and faces.

Average percent signal change for each stimulus condition is shown in Figure 3 and Table 1. Despite the fact that both the Lego objects and the Lego layouts were made of the same component materials, PPA response was significantly higher to the Lego layouts than to the Lego objects ($t[5] = 5.1$, $p < 0.001$ for the difference between Lego objects and layouts without animals), demonstrating that the PPA responds strongly to spatial layouts even when they are not real places that the subjects could have ever visited. The response to Lego layouts was not as high as the response to scenes depicting real places ($t[5] = 4.2$, $p < 0.01$ for the difference between empty rooms and layouts with animals), and the response to Lego layouts with animals was higher than the response to bare Lego layouts ($t[5] = 4.7$, $p < 0.01$). Possible reasons for these differences will be considered in the Discussion section. There was no difference in response between Lego objects and everyday objects ($t < 1$) or between the furnished rooms and empty rooms ($t < 1$). The latter result is a replication of our previously reported finding that PPA response does not depend on the presence of discrete objects in the scene (Epstein and Kanwisher, 1998).

Overall, activity was marginally higher in the 1-back task than in passive viewing ($t[5] = 2.1$, $p = 0.09$), and the interaction of task with stimulus type was marginally significant ($F[6,30] = 2.4$, $p = 0.052$). The nature of the latter interaction can be seen by examining Table 1: although activity was higher in the 1-back task than in passive viewing for all stimulus conditions, this difference was particularly large for the Lego scenes. For example, the difference in percent signal change between 1-back and passive viewing was 0.3 for empty rooms but 0.6 for Lego scenes with animals ($F[1,5] = 7.6$, $p < 0.05$ for the interaction). This pattern suggests that the PPA does not respond strongly to the Lego scenes unless subjects are required to attend closely to them, as they are when performing the 1-back task.

Experiment 3

Experiment 3 was designed to test the hypothesis that the PPA is involved in guiding or monitoring locomotion through the immediate environment. Four subjects viewed scenes under two different conditions (see Figure 4). In the movie condition, they viewed a sequence of photographs taken from a moving camera which gave them a vivid sense of forward motion. In the scene condition, they viewed a series of unrelated photographs. If the PPA were involved in guiding or monitoring locomotion through the local environment, then we predicted its response would be higher in the movie condition, because subjects have the impression that they are actually moving in this condition. Subjects also viewed faces and objects in this experiment. Average percent signal change within the PPA was 1.3% for the scenes, 0.9% for the movies, 0.4% for the objects, and 0.1% for the faces. Analysis of variance revealed that activity in the PPA was significantly higher in the "scene" condition than in the "movie" condition ($t[3] = 11.4$, $p < 0.01$). Thus, we found no support for the hypothesis that the PPA plays a role in guiding navigation through the immediate environment.

Experiment 4

In this experiment, we tested the hypothesis that the PPA is involved in encoding, using a variant of a paradigm that has been used by several other researchers (Tulving et al., 1994; Stern et al., 1996; Gabrieli et al., 1997). Subjects viewed photographs of scenes and faces under two different conditions (see Figure 5A). In

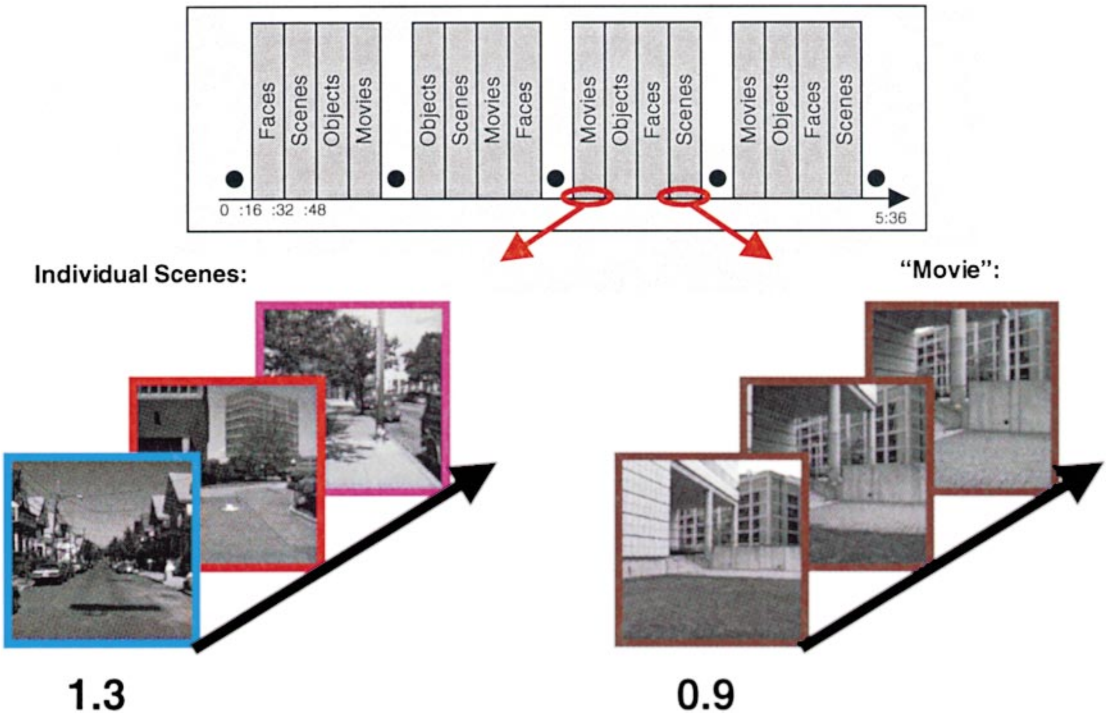


Figure 4. Design and Results of Experiment 3

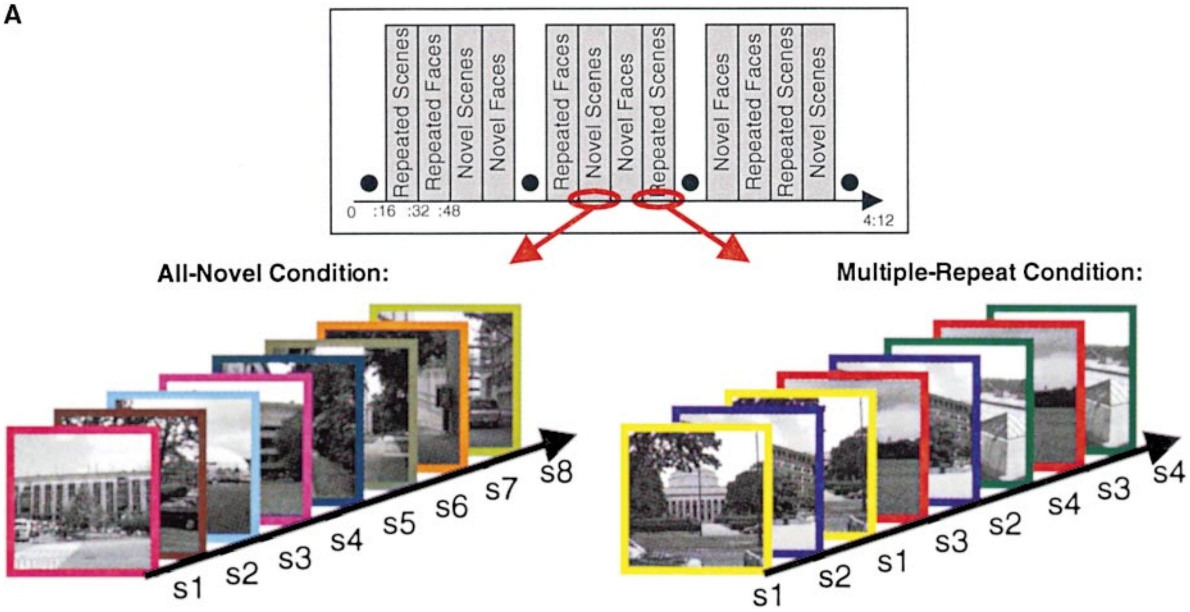
Top shows the series of conditons for a single scan; each of the four stimulus conditions occurred four times within the scan. During "scene" epochs, subjects saw a sequence of 20 unrelated snapshots. During "movie" epochs, subjects saw an ordered series of 20 photographs taken from a camera moving forward through a single, unchanging environment. Average percent signal change in the PPA was 1.3% during scene epochs, 0.9% during movie epochs, 0.4% during object epochs, and 0.1% during face epochs.

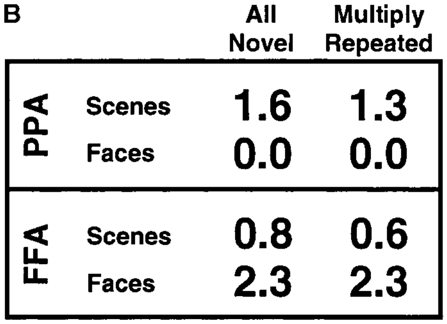
the *all-novel* condition, every photograph was different. These photographs did not repeat within the experiment, so every time the subject saw a photograph they were seeing it for the first time. In the *multiple-repeat* condition, the same four photographs were shown over and over again throughout a scan (though not always in the same order). If the PPA were involved in perceptual or mnemonic encoding, we predicted that its response would be higher in the all-novel condition, because there are more photographs to encode in this case. Use of both scenes and faces allowed us to examine whether any encoding effects occur for other stimulus types, or whether they are specific to scenes. In order to ensure that subjects attended to the stimuli in both conditions, they were required to perform a 1-back repetition detection task throughout the entire experiment.

Note that whereas the critical variable in Experiments 1 and 2 was the familiarity of the *place depicted*, the critical variable in this experiment is the novelty/familiarity of the *particular image*. Familiarity with a *place* implies that you have a representation of that place within your cognitive map. Familiarity with an *image* implies that you have processed this particular set of perceptual features before. One can view an unfamiliar image of a familiar place (as when an MIT student sees a picture of the MIT campus from a novel viewpoint) and one can also view a familiar image of an unfamiliar place (as when one repeatedly views photographs of landscapes one has never visited).

Results are shown in Figure 5B. Activity in the PPA was significantly higher for scenes than for faces ($t[6] = 9.6$, $p < 0.001$). In fact, consistent with our previous results, the response to faces was no greater than the response to a fixation point. In addition, the PPA responded significantly more to the novel stimuli than to the repeated stimuli ($t[6] < 3.8$, $p < 0.01$). This novelty advantage was found for the scenes ($t[6] = 10.4$, $p < 0.001$) but not for the faces ($t < 1$), and the interaction between novelty (novel versus repeated) and picture type (scene versus face) was significant ($F[1,6] = 8.7$, $p < 0.05$). Analysis of the behavioral data from the 1-back task indicated that the advantage for novel scenes could not be explained by presuming that subjects were attending more in this condition, as subjects performed the task equally well in the novel and repeated scene conditions (87.2% correct for the novel scenes, 82.9% for the repeated scenes, $t < 1$ for the difference), and reaction times in the two conditions were comparable (in fact, reaction times were 119 ms longer in the repeated condition, but this difference was not significant; $t[5] = 1.3$, $p > 0.25$). Thus, the PPA responds more strongly when there are more different scenes to encode but not when there are more different faces.

Table 2 shows the evolution of the difference between novel and repeated scenes over the time course of each scan. Within each individual scan, there were three epochs during which subjects viewed novel scenes and three epochs during which they viewed repeated scenes. At the beginning of each scan, *all* the scenes





		All Novel	Multiply Repeated
PPA	Scenes	1.6	1.3
	Faces	0.0	0.0
FFA	Scenes	0.8	0.6
	Faces	2.3	2.3

Figure 5. Design and Results of Experiment 4

(A) The top shows the series of conditions for a single scan. Within each all-novel epoch, subjects saw 18 photographs they had never seen before. Within multiple-repeat epochs, subjects saw the same four photographs repeatedly. (These four photographs also repeated across epochs within a single scan.)

(B) Average percent signal change for each condition in the PPA (top) and the FFA (bottom). A novelty advantage was found for scenes but not faces in the PPA. No similar novelty advantage was found for either scenes or faces in the FFA.

were novel to the subjects (even the ones that would eventually be repeated many times over). Thus, we would expect any novelty advantage to show up more strongly in the later epochs of the scan, when multiple viewings of the same four scenes in the multiply repeated condition causes them to be processed differently from the scenes in the all-novel condition. In fact, this is exactly what we observed. There was no difference in response between the first epoch of novel scenes and the first epoch of repeated scenes, demonstrating that repetition of stimuli five times within a single epoch was not sufficient to reduce the PPA response. In the second and third epochs, however, the response to the repeated scenes was significantly reduced compared to the response to the novel scenes.

Do such novelty effects occur only in the PPA, or can they be found in any regions of cortex specialized for processing a specific kind of visual information? To examine this question, we looked for novelty effects in the fusiform face area (FFA) (Kanwisher et al., 1997; McCarthy et al., 1997). The FFA has been demonstrated to respond selectively to faces; thus, one might expect to find greater response to novel compared to repeated faces in the FFA. We defined the FFA functionally using data from the same independent set of scans used to define the PPA. All contiguous voxels in the right fusiform gyrus that responded significantly more ($p < 10^{-4}$ Kolmogorov-Smirnov) to faces than to objects (chairs and cars) were included (see Kanwisher et al., 1997, 1998, for details). Results are shown in Figure 5B. The FFA responded significantly more to faces than scenes ($t[6] = 8.1$, $p < 0.001$) but responded no more to novel than to repeated stimuli ($t < 1.3$). Thus, not all high-level visual areas respond more to their preferred stimuli when they are novel than when they are repeated.

Table 2. Average Percent Signal Change for Novel and Repeated Scenes in Experiment 4, by Epoch within Scan

	Epoch 1	Epoch 2	Epoch 3	Average
Novel scenes	1.5	1.7	1.6	1.6 (0.5)
Repeated scenes	1.5	1.1	1.2	1.3 (0.5)
Novel-repeated	0.0	0.6***	0.4*	0.3**

Significance levels: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Variances are in parentheses.

Discussion

The experiments presented in this paper were designed to test three possible functions of the PPA: (1) place recognition, (2) planning of routes through the local or distal environment, and (3) place encoding. We found no evidence that the PPA is involved in place recognition or route planning and some evidence that it is involved in either perceptual or mnemonic encoding of new place information.

Experiment 1 tested the hypothesis that the PPA is involved in place recognition. This experiment was motivated in part by the neuropsychology literature. A number of patients with right hemisphere medial temporooccipital lesions display a striking inability to use the visual appearance of places and landmarks for purposes of orientation (Whiteley and Warrington, 1978; Landis et al., 1986; Habib and Sirigu, 1987; McCarthy et al., 1996; Aguirre et al., 1998a; Bohbot et al., 1998; Aguirre and D'Esposito, 1999). This suggests that there might be a cortical region dedicated to place/landmark recognition analogous to the FFA, which is thought to play a critical role in face recognition (Haxby et al., 1994; Kanwisher et al., 1997, 1998; McCarthy et al., 1997). In their report of four patients suffering from topographical disorientation, Habib and Sirigu (1987) found a common lesion site in right parahippocampal cortex that is consistent with the anatomical location of the PPA.

Given its strong selectivity for visual place information, the PPA is clearly a candidate place recognition region. In particular, the PPA may have the specific role of determining one's current location by linking the current visual scene to one's stored cognitive map of the world. If this is the case, one might expect its response to be higher to photographs of familiar places than to photographs of unfamiliar places, as the locations of the former are known while the locations of the latter are not. Alternatively, one might expect the PPA to respond *less* strongly to photographs of familiar places. Neurons in the inferior temporal cortex and superior temporal sulcus of the monkey brain have been observed to both increase (Rolls et al., 1989) and decrease (Miller et al., 1991; Li et al., 1993) their firing rate as a stimulus becomes more familiar. If the photographs of familiar places activate representations that are sparser or more sharply tuned than those activated by unfamiliar places, this might be reflected in lower overall activity in the PPA for the familiar places. Thus, the place recognition hypothesis predicts that the response to familiar places should be either higher or lower than the response to unfamiliar places but is unlikely to be the same.

The results of Experiment 1 failed to support this prediction. PPA response was just as high to photographs of the unfamiliar college campus as it was to the photographs of the familiar (and presumably, highly overlearned) college campus. Furthermore, the PPA showed none of the reduction in response for familiar compared to unfamiliar scenes that one might expect if the representations activated by photographs of familiar places were sparser than those activated by unfamiliar places (Miller et al., 1991; Li et al., 1993). Thus, the overall activity of the PPA was not affected by the familiarity of the place depicted in the scene. Note that, as in all imaging studies, this lack of a difference in response does not preclude the possibility that the population codes within the PPA may be different for familiar and unfamiliar scenes; however, any such differences are not reflected in the overall response of the region.

A secondary purpose of Experiment 1 was to examine the response of the PPA to individual landmarks such as buildings. In our earlier work, we observed that the PPA responded more to buildings than to common objects (Epstein and Kanwisher, 1998). Subsequent investigations have revealed that this is the case even when the nonbuilding items are ships, trains, and other objects comparable in size to the buildings (R. E. and N. K., unpublished data). Other researchers have identified building-selective voxels in locations near enough to the PPA to be potentially overlapping (Ishai et al., 1997, Neuroimage, abstract; Aguirre et al., 1998a, 1998b) but did not compare the response to buildings to the response to full scenes. In the present experiment, the PPA response to scenes was significantly higher than the response to individual landmarks cut out from their spatial context.

In contrast to the scene response, the response to landmarks was significantly higher when they were familiar. We have proposed that the PPA responds strongly to landmarks because subjects experience them not as detached objects but as stable structures that help define the space around them (Epstein and Kanwisher, 1998). The finding of greater response to familiar landmarks is consistent with this account, because subjects would be more likely to process familiar landmarks as partial scenes (rather than as detached objects) if they had in the past experienced them as such. In fact, viewing of a familiar landmark might cause subjects to imagine the rest of the scene, which would lead to greater activation in the PPA (O'Craven and Kanwisher, submitted). Further supporting this account is the fact that the response to the landmarks was reduced when subjects performed the 1-back task (in contrast to the other stimulus conditions, where the response was higher in this task). Performance of this task requires subjects to attend closely to the stimulus, making it more likely that subjects will focus on the details of the building rather than imagining the scene around it.

The failure to find a familiarity effect for scenes in Experiment 1 suggested that spatial layout information alone, even in the absence of any plausible sense of place familiarity, might be sufficient to activate the PPA. In Experiment 2, we conducted a stronger test of this hypothesis by comparing PPA response to artificial "scenes" made out of Legos with its response to Lego objects. The former had a geometric structure similar to that of real scenes, but were clearly *not* real places in the world that subjects could have ever visited. Despite the fact that the Lego scenes and Lego objects were made of the same materials, the PPA response was significantly higher to the Lego scenes, consistent with our original claim that PPA activity correlates strongly with the presence of a particular kind of geometric structure in the stimulus (Epstein and Kanwisher, 1998) rather than with higher-level navigational or recognition processes. In particular, this result indicates that the PPA is unlikely to be directly involved in matching of the current scene to one's stored cognitive map of the world, because the PPA responds strongly to photographs of "places" that subjects know they have never visited.

However, it is important to note that the response to the Lego scenes in the PPA was also significantly lower than the response to the real scenes. While in principle this may mean that at least some of the PPA response to real scenes corresponds to the activity of place recognition mechanisms, there is another possible explanation, which we favor. Despite our efforts, the Lego scenes were probably not as immediately comprehensible as places (i.e., spaces that one can be in) as the real scenes. Subjects had only 800 ms to process each photograph before the next one appeared, and this might not have been enough time to interpret the spatial structure of some of the Lego scenes. Supporting this account is the fact that the PPA responded significantly more to Lego scenes with animals than to bare Lego scenes without any objects. In contrast, the response to the real scenes containing objects (furnished rooms) was not any greater than the response to the real scenes without discrete objects (empty rooms), a replication of our previous results (Epstein and Kanwisher, 1998). The presence of the animals in the Lego scenes was specifically intended to enhance the subject's ability to perceive the geometric structure of these stimuli, and some subjects did indeed report that they had such an effect. Thus, the greater response to the Lego scenes with animals suggests that it is the interpretability of the layout of the scene rather than the recognizability of the place depicted that is the critical factor in determining the level of PPA activity.

Thus, taken together, Experiments 1 and 2 provided little evidence that the PPA is involved in place recognition in the sense of matching the perceptual input to a particular stored representation of a known place. The lack of a familiarity effect for scenes further demonstrates that the PPA is very unlikely to play a direct role in planning routes to distant locations, since one cannot plan routes from locations one does not know. Although some earlier studies have shown general involvement of the medial temporal lobe in navigation tasks (Maguire et al., 1996; Ghaem et al., 1997), others have suggested that only the more anterior regions such as the right hippocampus are involved in route planning per se (Maguire et al., 1997, 1998; but see Aguirre et al., 1996). The present results extend this work by demonstrating that the PPA is not involved in distal route planning.

Experiment 3 was designed to test the possibility that the PPA plays a more immediate role in navigation: guiding or monitoring locomotion through the local (i.e., currently visible) environment. Activity when viewing a sequence of unrelated scenes was compared to activity when subjects viewed a "movie" depicting forward motion through a single environment. Despite the fact that subjects reported that the movie condition was much more interesting and engaging than the unrelated-scene condition, PPA response was significantly higher in the unrelated-scene condition. Thus, whereas the results of Experiments 1 and 2 argue against a role for the PPA in planning routes through the distal environment, the results of Experiment 3 argue against a role for the PPA in the specific navigational task of guiding or monitoring locomotion through the local environment.

However, we should note that these conclusions must be treated with some caution, as the snapshot and movie conditions were not equated for encoding demands. In particular, there was more overlap between the individual images for the movies than for the snapshots, which may account for the smaller response to the movies. In Experiment 4, we measured the encoding effect directly and found it to be roughly equivalent in strength (0.3% difference between novel and repeated scenes) to the difference between the unrelated scene and movie conditions in Experiment 3 (0.4%). Thus, it is possible that the encoding effect in Experiment 3 masked a navigational effect operating in the opposite direction, though any such navigation effect must have been quite small in magnitude.

Experiment 4 explicitly examined the role of the PPA in the encoding of novel stimuli. Activity when viewing a series of novel photographs was compared with activity when viewing the same small set of photographs repeated over and over again. When the stimuli were scenes, the PPA response was greater in the all-novel than in the repeated condition. These results are consistent with PPA involvement in encoding new perceptual information about the appearance and layout of scenes, because there are more scenes to encode in the former condition. This novelty advantage was found only in the later epochs of the scan, after the repeated scenes had already been encoded. No similar novelty advantage was observed for faces in the PPA, nor were novelty effects for either faces or scenes observed in the FFA (although this last result may depend on task; see Gauthier et al., 1998, Neuroimage, abstract).

It is interesting to compare the results of Experiments 1 and 4. In Experiment 1, the novelty/familiarity of the depicted place was varied. In contrast, in Experiment 4, the novelty/familiarity of the depicted place was held constant (i.e., all the scenes were unfamiliar places) while the novelty/familiarity of the stimuli themselves was varied. The PPA appears to be sensitive to the latter manipulation but not the former. In other words, experience with the particular set of perceptual inputs present in a scene affects PPA response, but experience with the place represented by the scene does not. Taken together with the results of Experiment 2, these results suggest that the PPA is more sensitive to the perceptual aspects of the stimulus than to higher-level information about the stimulus such as its location in the real world.

The results of Experiment 4 are generally consistent with other fMRI experiments that have found greater parahippocampal activation when subjects view novel compared to repeated scenes (Stern et al., 1996; Gabrieli et al., 1997) and subsequently remembered compared to subsequently forgotten scenes (Brewer et al., 1998). Based on these results, some researchers (Stern et al., 1996; Gabrieli et al., 1997) have proposed that parahippocampal cortex plays a general role in encoding visual stimuli. Counter to this proposal, our experiments have consistently failed to find any evidence that the PPA plays a role in processing face information (Epstein and Kanwisher, 1998), a finding that is consistent with neuropsychological results that have demonstrated a dissociation between face memory and topographical memory (Maguire and Cipolotti, 1998). Insofar as the PPA overlaps with the putative encoding regions reported by Stern et al. (1996) and Gabrieli et al. (1997), the present results suggest that at least some of the previously observed parahippocampal encoding effects may actually be specific to scenes. However, other regions within parahippocampal cortex (or elsewhere in the medial temporal lobes) may be involved in encoding faces and other nonscene information (Haxby et al., 1996; Clark et al., 1998; Kelley et al., 1998). In particular, a recent event-related fMRI study found activity in a number of cortical regions including left parahippocampal cortex that correlated with subsequent memory for individual words (Wagner et al., 1998). Although the effects were small, they provide evidence that some part of parahippocampal cortex plays a role in encoding verbal information. Whether the regions activated in the Wagner et al. (1998) study overlap with the PPA has yet to be determined. If they do overlap, it would suggest that the PPA is involved in encoding at least some kinds of nonspatial information, perhaps by encoding the spatial–temporal context in which individual verbal events are experienced.

While all of the above results implicate parahippocampal cortex in encoding, they do not allow us to determine whether it is involved in the bottom-up perceptual analysis of the stimulus or the entry of this information into long-term memory (or both). The greater response to novel compared to repeated scenes in Experiment 4 (and in the experiments of Stern et al. [1996] and Gabrieli et al. [1997]) may be due to the fact that there are more scenes to enter into memory in the novel condition, or it may simply indicate that more perceptual processing occurs for the novel than for the repeated scenes. Insofar as stimuli that receive more perceptual processing are also more likely to be encoded into memory, the results of Brewer et al. (1998) and Wagner et al. (1998) could also be explained in terms of either perceptual or mnemonic processes. It is unclear whether neuroimaging can resolve this issue.

However, data from neuropsychology can provide important clues about PPA function. There are at least two reports (Ross, 1980; Habib and Sirigu, 1987) of patients who can find their way around familiar environments but show a complete inability to learn new environments. Based on this finding, Aguirre and D'Esposito (1999) have suggested that there may be distinct cortical regions dedicated to (1) recognizing places/landmarks and (2) encoding new place information. Consistent with this hypothesis, Aguirre and his collaborators have identified building-selective voxels within the lingual gyrus (Aguirre et al., 1998b). Although these voxels are very close to the PPA, the Talairach coordinates are different enough to suggest that they may compose an anatomically distinct region. If so, it may be that this "lingual landmark area" (LLA) (Aguirre et al., 1998b) is the place recognition module predicted from the cases of landmark agnosia, whereas the PPA is more involved in encoding place information into memory. Alternatively, there may be no functional or anatomical distinction between these two regions of the brain. In this view, the LLA/PPA carries out the bottom-up perceptual analysis of the appearance of places (and perhaps additional processes necessary for memory encoding), but the actual place memories are stored elsewhere in the brain. Place recognition would then require both perceptual analysis (in the LLA/PPA) and comparison of that information to stored place memories (in as-yet-unspecified brain regions). This hypothesis is consistent with the facts that (1) damage to the lingual/parahippocampal region results in landmark agnosia, and (2) the present experiments found no evidence that the PPA responds more to pictures of familiar than unfamiliar places. Determining which of these hypotheses is correct may require behavioral testing of patients with damage restricted to either the PPA or the LLA.

Experimental Procedures

Subjects

Eight subjects (five male, three female) were run in Experiment 1, six (two male, four female) in Experiment 2, four (one male, three female) in Experiment 3, and seven (three male, four female) in Experiment 4. The data from five additional subjects (one in Experiment 2, three in Experiment 3, one in Experiment 4) were discarded before analysis because of excessive head motion. All subjects were right-handed and had no known history of neurological impairment; ages ranged from 18 to 39. For Experiment 1, four of the subjects were MIT students unfamiliar with the Tufts University campus, and four were Tufts University students unfamiliar with the MIT campus. For Experiments 2–4, subjects were drawn from the MIT community.

Procedure

Experiments 1 and 2

MR data for each subject were obtained from four scans within the same scan session. In two of the scans, subjects simply watched the stimuli passively. In the other two scans, subjects performed a 1-back repetition detection task in which they were required to press a button whenever they saw two identical pictures in a row. Each scan was 5 min and 36 s long and consisted of sixteen 16 s epochs during which subjects viewed digitized black-and-white photographs interleaved with five epochs during which the screen was blank except for a fixation point (see Figure 2A). During each picture epoch, 20 different photographs of the same type were shown (with one or two consecutive repetitions per epoch in the 1-back task). Each photograph was presented for 300 ms followed by a blank interval of 500 ms. There were two epochs for each of the eight stimulus types within each scan; epoch order was counterbalanced as described previously (Epstein and Kanwisher, 1998) by running each subject on two versions of each experiment.

Stimuli in Experiment 1 were digitized black-and-white photographs of (1) the MIT campus, (2) the Tufts campus, (3) landmarks from the MIT campus, (4) landmarks from the Tufts campus, (5) common objects, and (6) faces of people unknown to the subjects. The landmark stimuli consisted of photographs of buildings cut out from their surrounding context and placed on a white background. The MIT scenes and landmarks were familiar to the four MIT subjects but the Tufts scenes and landmarks were not; the opposite was true for the four Tufts University students. There were also two other stimulus conditions designed to test other hypotheses; these will be reported elsewhere. Stimuli in Experiment 2 were digitized black-and-white photographs of (1) indoor scenes of unfamiliar rooms filled with furniture; (2) the same rooms photographed from the same angle after all of the objects had been removed; (3) "scenes" made of Lego blocks; (4) the same scenes with small toy animals added; (5) objects made of Lego blocks; (6) common, everyday objects; and (7) faces of people unfamiliar to the subjects. An eighth condition designed to test an unrelated hypothesis was also included.

Experiment 3

The basic procedure was the same as in Experiments 1 and 2, with the following exceptions. MR data were obtained for each subject from two scans from the same scan session. Photographs were shown for 800 ms each without any blank space between photographs. There were four stimulus conditions (movies, scenes, objects, and faces); thus, each scan contained four different epochs for each stimulus condition. Subjects were instructed to view the stimuli attentively.

During movie epochs, subjects viewed sequences of black-and-white photographs shot from a camera moving through an outdoor environment. These photographs were viewed in the sequence in which they were taken, and the close connection between successive photographs gave subjects a powerful sense of forward motion through a single, unchanging environment (as if they were watching a movie). During scene epochs, subjects viewed photographs of unrelated scenes. These photographs were the same as those in the various movie epochs, but they were presented in a pseudorandom order to ensure that each scene had no connection to the preceding and succeeding scene, and that no more than three photographs from the same environment were shown in each scene epoch (See Figure 4). In the other two stimulus conditions, subjects viewed photographs of objects and faces.

Experiment 4

The basic procedure was the same as in Experiments 1 and 2, with the following exceptions. MR data were obtained for each subject from two scans from the same scan session. Each scan was 4 min and 12 s long and consisted of twelve 16 s epochs during which subjects viewed photographs interleaved with four fixation epochs. There were four stimulus conditions (novel scenes, novel faces, multiply repeated scenes, multiply repeated faces); thus, each scan contained three different epochs for each stimulus condition. Subjects performed the 1-back task in both scans. We expected that this task would be, if anything, more difficult in the multiply repeated conditions than in the novel conditions (because of proactive interference), so a greater activation in the novel condition could not be an artifact of attention or effort. Epoch order was counterbalanced across two different versions of the experiment (ABCD-BCDA-CBAD for version 1, DABC-ADCB-DCBA for version 2). Four subjects were run on version 1 and three on version 2. Behavioral data for one subject were lost due to a computer error.

In each novelty epoch, subjects saw 18 different photographs of the same type. Two of the photographs were presented twice in a row to ensure that subjects were performing the 1-back task. Photographs did not repeat across epochs or scans, so altogether subjects saw a total of 108 different scenes and 108 different faces in the two novelty conditions. In the multiply repeated conditions, subjects saw the same 4 photographs over and over (though not always in the same order). These photographs were the same across epochs in the same scan but differed across scans, so altogether subjects saw a total of 8 different scenes and 8 different faces in the two multiple-repeat conditions. Within each epoch, two of the photographs were presented twice in a row to ensure that subjects were performing the 1-back task.

MRI Data Acquisition

Scanning was done at the MGH-NMR Center at Charlestown, MA, using a bilateral surface coil which provided a high signal-to-noise ratio in posterior brain regions. A bite bar was used to minimize head motion. Standard imaging parameters were used (TR = 2 s, TE = 70 ms, flip angle = 90°, 180° offset = 25 ms) as have been described previously (Kanwisher et al., 1997; Epstein and Kanwisher, 1998). Ten or twelve 6-mm-thick near-coronal slices covered the anterior portion of the occipital lobe and the posterior portion of the temporal and parietal lobes. Either 168 (Experiments 1–3) or 128 (Experiment 4) functional images were collected for each slice in each scan. All subjects were run on a 3T scanner, except for one subject in Experiment 2, who was run on a 1.5T scanner.

Data Analysis

For each subject, the data from all the runs in each experiment were averaged together. Then the time course of MR signal intensity was extracted from each subject's PPA (averaging over all voxels within the region of interest). Because the order of the conditions was not counterbalanced within each subject in Experiment 4, the data from this experiment was corrected for linear drift. The PPA was defined using data from a separate set of scans from the same subject and scan session, and included all contiguous voxels in the collateral sulcus region for which a Kolmogorov-Smirnov test found higher levels of activation at the significance level of $p < 10^{-4}$ for scenes compared to the average response to faces and objects. In most subjects, this criterion resulted in a region of interest that was consistent and limited to parahippocampal cortex. In a small number of subjects, parahippocampal activation was found to be contiguous with activations in the lingual and fusiform gyrus. Because we wished to maintain a definition of the PPA that was anatomically consistent across subjects and experiments, we did not include these occasional posterior activations in our definition of the PPA. The percent signal change in the PPA was calculated for each subject, experiment, stimulus condition, and task, using the average signal intensity during fixation epochs for the same subject, experiment, and task as a baseline. Because the fMRI response typically lags 4–6 s behind the neural response, we treated the first functional image of each epoch as belonging to the condition of the previous epoch and omitted the next two images (during the transition between conditions) from the analysis. ANOVAs across subjects were run on the average percent signal change in each of the conditions in each experiment. Although the Kolmogorov-Smirnov test can in principle reflect a difference in variance rather than a difference in mean (Aguirre et al., 1998c), these ANOVAs confirmed that the average MR signal in the regions of interest selected by this procedure was indeed significantly higher during viewing of scenes than during viewing of faces or objects in each experiment in this paper, as it was in each experiment in our previous report (Epstein and Kanwisher, 1998). Because data were analyzed within independently defined regions of interest, no correction for multiple voxelwise comparisons was made.

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