

Viewpoint-Specific Scene Representations in Human Parahippocampal Cortex

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Summary

The “parahippocampal place area” (PPA) responds more strongly in functional magnetic resonance imaging (fMRI) to scenes than to faces, objects, or other visual stimuli. We used an event-related fMRI adaptation paradigm to test whether the PPA represents scenes in a viewpoint-specific or viewpoint-invariant manner. The PPA responded just as strongly to viewpoint changes that preserved intrinsic scene geometry as it did to complete scene changes, but less strongly to object changes within the scene. In contrast, lateral occipital cortex responded more strongly to object changes than to spatial changes. These results demonstrate that scene processing in the PPA is viewpoint specific and suggest that the PPA represents the relationship between the observer and the surfaces that define local space.

Introduction

A number of neuroimaging experiments have revealed regions in human occipitotemporal cortex that respond preferentially to certain kinds of visual stimuli, including faces (Haxby et al., 1996; Kanwisher et al., 1997a; McCarthy et al., 1997; Puce et al., 1995), objects (Kanwisher et al., 1997b; Malach et al., 1995), bodies (Downing et al., 2001), houses (Aguirre et al., 1998; Ishai et al., 1999), and scenes (Epstein and Kanwisher, 1998; Kohler et al., 2002). For example, Epstein and Kanwisher (1998) demonstrated that a region in posterior parahippocampal cortex responds significantly more strongly in fMRI to environmental scenes than to other kinds of meaningful visual stimuli. In particular, this “parahippocampal place area” (PPA) responds more strongly to photographs of landscapes, cityscapes, and rooms than to photographs of faces, objects, or scrambled scenes. Thus, the PPA activates when subjects view stimuli that

convey information about the geometry of surrounding space. From these results, it was hypothesized that the PPA processes information about the spatial structure of the currently visible environment (Epstein et al., 1999). Neuropsychological studies have confirmed the critical involvement of parahippocampal cortex in scene perception and spatial navigation (Aguirre and D’Esposito, 1999; Bohbot et al., 1998; Epstein et al., 2001; Habib and Sirigu, 1987).

One issue that has not been resolved is whether the PPA represents scenes in a viewpoint-specific or viewpoint-invariant manner. In the former case, the PPA would process two views of the same scene as if they were representationally distinct, while in the latter case it would process the same two views as if they were representationally identical. Distinguishing between these two scenarios is important for understanding the role of the PPA in spatial processing and navigation. In particular, if the PPA processes scene geometry in a viewpoint-independent manner, this would suggest that its primary function is representation of the intrinsic geometry of different places, perhaps as a precursor to their identification. In contrast, if the PPA processes scene geometry in a viewpoint-dependent manner, this would suggest that its primary function is to represent the spatial relationship between the body and the set of connected surfaces that comprises the current scene. Such a computation might be a necessary precursor to calculating the location and orientation of the body relative to a map of the world (Burgess, 2002)—information encoded by place cells in the hippocampus (Best et al., 2001; O’Keefe and Nadel, 1978) and head direction cells in the postsubiculum, retrosplenial cortex, and other regions (Muller et al., 1996; Taube, 1998).

The current study addressed this issue by use of an event-related fMRI adaptation paradigm. Subjects viewed events consisting of two successively presented photographs of tabletop scenes. In the critical conditions, the two photographs depicted either (1) different scenes or (2) the same scene from different viewing angles. Previous blocked (Epstein et al., 1999; Stern et al., 1996) and event-related (Kirchhoff et al., 2000) fMRI studies have demonstrated reduced response (i.e., adaptation) in parahippocampal cortex for repeated compared to novel scenes, but have not examined the effects of repeating or changing specific aspects of those scenes. Based on previous neuroimaging (Buckner et al., 1998; Grill-Spector et al., 1999, 1998; Henson et al., 2000; Jiang et al., 2000; Kourtzi and Kanwisher, 2001; Schacter and Buckner, 1998) and neurophysiological (Desimone, 1996; Li et al., 1993; Miller et al., 1991; Muller et al., 1999) results, we expected that the regional event-related fMRI response to each scene pair would be greater if the scenes differed along an informational dimension processed by the region than if they did not. This prediction was based on the hypothesis that the subset of neurons engaged by the two photographs would be nonidentical in the “different” condition but largely overlapping in the “same” condition, leading to a greater amount of neural adaptation and reduced fMRI

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response to the second photograph in the latter case (see Grill-Spector and Malach, 2001). We therefore predicted that the PPA would respond more strongly to complete scene changes than to viewpoint changes if it represented scenes in a viewpoint-invariant manner, but would respond equally strongly to both kinds of changes if it represented scenes in a viewpoint-specific manner. Additional conditions examined the effects of changing objects within the scene. Neural activity was monitored in three occipitotemporal regions: the PPA, the “fusiform face area” (FFA; Kanwisher et al., 1997a), and the “lateral occipital complex” (LO; Malach et al., 1995).

A pilot experiment demonstrated that the PPA responds just as strongly to tabletop scenes as it does to photographs of landscapes or rooms (see Experimental Procedures) and responds significantly more strongly to tabletop scenes than to common objects. This suggests that tabletop scenes are just as efficacious as larger-scale scenes for engaging the processing mechanisms within the PPA and thus are adequate stimuli for investigating the nature of these processing mechanisms.

Results

Experiment 1

Fifteen subjects were scanned with functional magnetic resonance imaging (fMRI) while viewing visual events in which two photographs of tabletop layouts were presented in rapid succession. The two photographs in each event had one of four possible relationships to each other: (1) they could be completely identical (no-change condition); (2) they could depict the same layout from the same viewing angle, but with a different prominent central object (object-change condition); (3) they could depict the same layout with the same central object, but shown from different viewpoints (viewpoint-change condition); or (4) they could show the same central object placed in different environments (place-change condition) (Figure 1). This design allowed us to measure the response in each region of interest (ROI) when the two scenes differed in (1) their identity and intrinsic spatial structure (place-change condition), (2) the implied egocentric spatial relationship between the observer and the scene (place-change and viewpoint-change conditions), (3) the identity and/or appearance of the central object in the scene (object-change condition).

In separate blocks, subjects either reported whether the two scenes differed in their central object (monitor-object task) or whether they depicted different tabletop layouts (monitor-place task). Subjects were highly accurate in both tasks (monitor-object task, $M = 95.7\%$; monitor-place task, $M = 96.2\%$). The high level of accuracy in the monitor-place task indicates that subjects were able to successfully identify that the two photographs depicted the same layout in viewpoint-change events but depicted different layouts in place-change events. Analysis of variance revealed that performance did not differ between the two tasks ($F < 1$) but did differ between the four change conditions [$F(3,36) = 5.3, p < 0.01$]. However, post hoc paired comparisons between the four change conditions failed to substanti-

ate change-related differences (all $ps > 0.1$, Bonferroni corrected), except for marginally better performance in the no-change condition compared to the viewpoint-change condition ($p = 0.07$, Bonferroni corrected). Although subjects were not required to make a speeded response, reaction times to correct trials were recorded. Subjects responded more quickly in the monitor-object task ($M = 570$ ms) than in the monitor-place task ($M = 654$ ms). Analysis of variance revealed that this difference was significant [$F(1,12) = 10.7, p < 0.01$], as were differences between the four change conditions [$F(3,36) = 17.9, p < 0.001$]. The latter effect was due to faster performance in the no-change condition ($M = 515$ ms) compared to the other three conditions ($M = 628$ ms for object changes, 648 ms for viewpoint changes, 656 ms for place changes; $p < 0.001$ Bonferroni corrected for all three paired comparisons relative to the no-change condition). The faster response to no-change trials might be interpreted as evidence for viewpoint-specific priming for scenes (Tarr and Pinker, 1989); however, insofar as the stimuli were physically identical in this condition, it may reflect a “fast same” effect (St. James and Eriksen, 1991). Importantly, RTs did not differ significantly between the object-change, viewpoint-change, and place-change conditions.

Neural activity was measured in three stimulus-selective regions in the right hemisphere: the parahippocampal place area (PPA), the fusiform face area (FFA), and the lateral occipital complex (LO), which were defined in each subject using data from independent localizer scans (Figure 2). The average event-related regional response to each of the four change conditions was calculated (for each subject, averaging across both tasks; task-related differences are discussed below). Differences between conditions were tested by planned comparisons between the levels of activation at the peak of the event-related response (Figure 3). Strikingly, the PPA responded equivalently to place changes and viewpoint changes ($t < 1$). Furthermore, PPA response to place and viewpoint changes was greater than its response to object changes [place versus object: $t(13) = 3.5, p < 0.01$; viewpoint versus object: $t(13) = 2.5, p < 0.05$].

In contrast, neither the FFA nor LO showed this preference for spatial changes over object changes. Indeed, LO showed a preference for object changes, responding significantly more strongly to object changes than to place changes [$t(11) = 2.5, p < 0.05$], and also more strongly on average to object changes than to viewpoint changes (although the latter difference was not significant; $t = 1.8, n.s.$). The response to place and viewpoint changes was equivalent in LO (both $t < 1$). No significant differences between the object-, viewpoint-, and place-change conditions were observed in the FFA.

Figure 4 (left) illustrates the difference in response pattern between the three regions of interest. For each region, the peak response for object, viewpoint, and place changes relative to the peak response of the no-change condition is plotted. Analysis of variance revealed a significant region \times change-type interaction between the PPA and the FFA [$F(2,24) = 6.7, p < 0.01$] and between the PPA and LO [$F(2,20) = 6.1, p < 0.01$], but not between the FFA and LO ($F < 1.3$). Thus, the PPA, FFA, and LO are preferentially sensitive to different kinds of information within a scene: the PPA responds

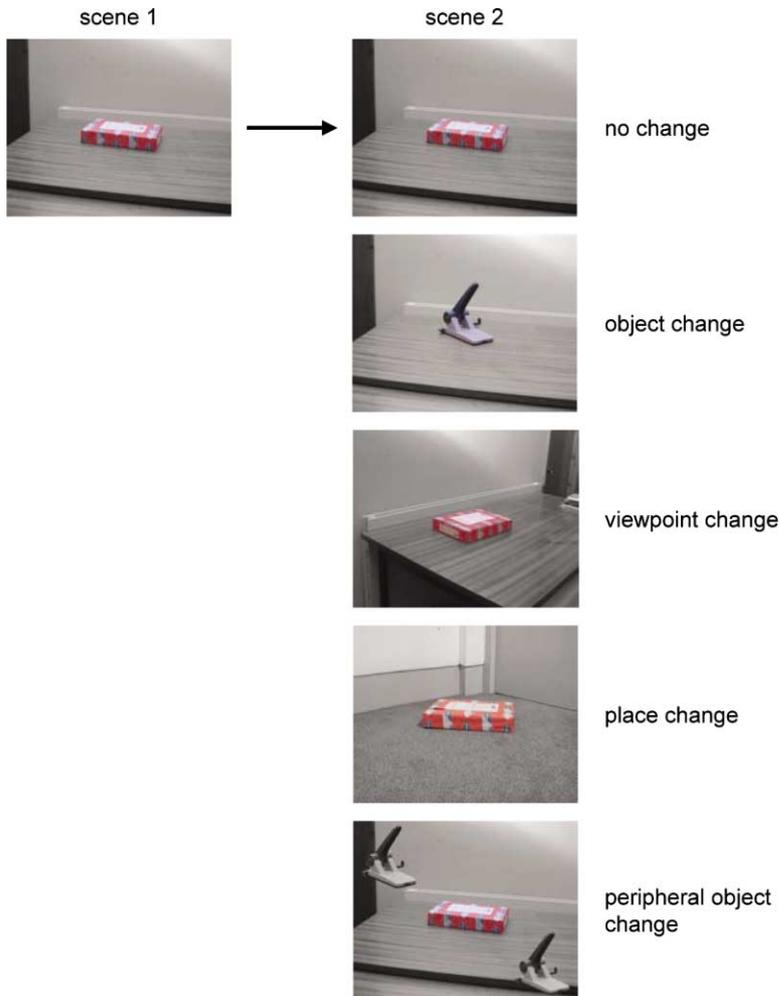


Figure 1. Examples of Stimuli Used in the Two Versions of the Experiment

In each trial, two tabletop or partial room scenes were shown. The response to the second scene was predicted to be greater when it contained novel information that was not present in the first scene than when it did not. Thus, it was possible to measure regional sensitivity to different kinds of novel information by systematically varying the relationship between the first and second scenes. Experiment 1 examined the no-change, object-change, viewpoint-change, and place-change conditions. Experiment 2 examined the no-change, object-change, place-change, and peripheral object-change conditions.

more strongly when the first and second scene differ in terms of their spatial information than when they differ in their component objects, while the FFA and LO do not show this preference. Indeed, LO tends to respond more strongly to object changes than to spatial changes, consistent with its putative role in processing the shapes of individual objects (Grill-Spector et al., 2001; Kanwisher et al., 1997b; Kourtzi and Kanwisher, 2001; Malach et al., 1995).

The response in all three change conditions was greater than the response in the no-change condition in the PPA (all $t_s > 2.4$, all $p_s < 0.05$) and the FFA (all $t_s > 2.4$, all $p_s < 0.05$). This result is not surprising given that the two photographs were visually different in the change trials but visually identical in the no-change trials. Thus, the second photograph likely recruited more attentional resources in change trials than in no-change trials. However, the reduced response in the no-change trials might also be due to priming of the “base” scenes, which were presented more often over the course of the experiment than the other scenes (Henson et al., 2000). Insofar as the base scenes were presented twice in the no-change trials but only once in the change trials, priming might lead to faster reaction times and reduced PPA response for no-change trials. Note that even if such long-term (crosstrial) priming effects were present

in the current experiment, they related to the number of times a given view was repeated, rather than the number of times a given place was repeated. Thus, like the short-term (within-trial) adaptation effects, any such priming effects operate in a viewpoint-specific manner.

Experiment 2

Insofar as information about object identity was always obtained from the center of the visual field while information about space was largely obtained from the periphery in Experiment 1, the present results might be explained in terms of differential processing of central versus peripheral visual information. Indeed, Levy et al. (2001) have argued that a house-selective region corresponding to the PPA is preferentially involved in processing information from the periphery of the visual field. In Experiment 2, we examined whether differences in the retinotopic location of the stimulus changes could explain the present results.

Fourteen new subjects were run in this experiment, which was identical to the first experiment except for the addition of a new condition, in which the second image of each event differed from the first by the appearance of two large grayscale objects in the corners of the scene (peripheral object-change condition; Figure 1). This condition replaced the viewpoint-change condi-

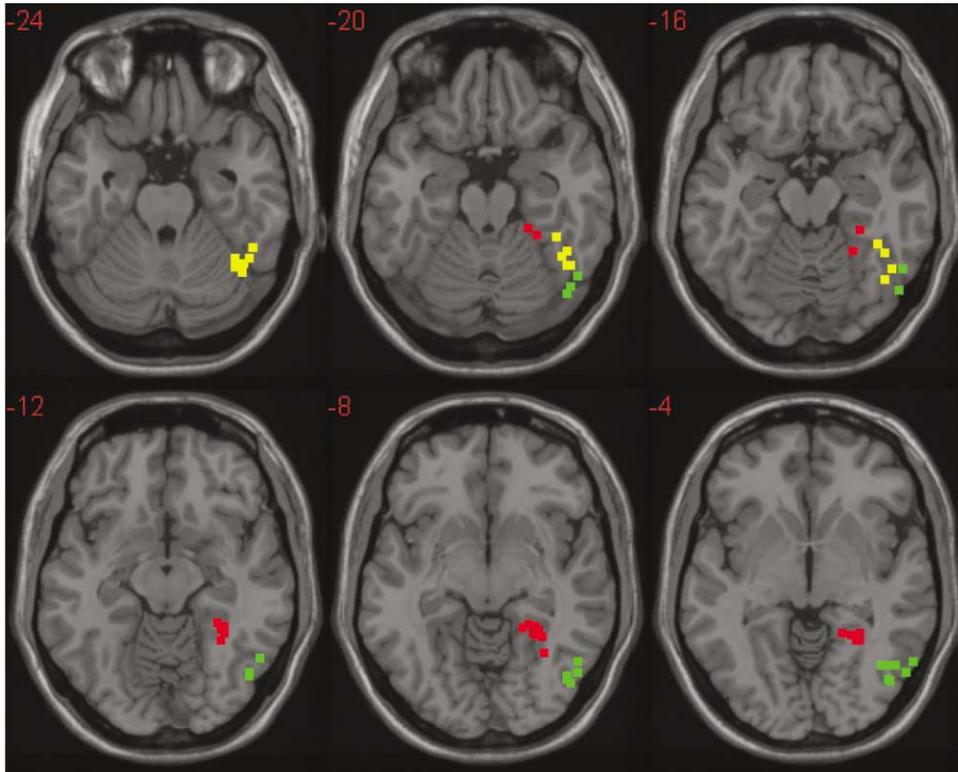


Figure 2. Regions of Interest

Location of the parahippocampal place area (red squares), fusiform face area (yellow squares), and lateral occipital complex (green squares) in the right hemisphere in both experiments, plotted onto axial slices of a reference brain in standard space. Right hemisphere is on the right. Each square represents one subject. In subjects where more than one peak voxel was observed, the average of the peaks is plotted. There is a very high degree of consistency in the anatomical location of the PPA, FFA, and LO across subjects. (Note: coregistration of the reference brain with the peak voxels is only approximate; thus, some of the FFA peaks in the fusiform gyrus are inaccurately plotted in the cerebellum in this figure.)

tion of Experiment 1. If the results of Experiment 1 can be explained simply by differential sensitivity to central versus peripheral changes in the PPA and LO, then we predicted that the PPA would respond more strongly to peripheral object changes than to central object changes, while LO would show the opposite pattern. In contrast, if the critical difference between the two regions is differential processing of spatial versus object information, then there would be little difference between the two object-change conditions in either region, because object information changes in both conditions while spatial information changes in neither.

Behavioral data were collected from 11 of the 14 subjects. Data from an additional three subjects were lost due to equipment failure. As in the previous experiment, subjects performed highly accurately in both tasks (monitor-object task, $M = 93.9\%$; monitor-place task, $M = 94.2\%$). Analysis of variance revealed that performance did not differ between the two tasks ($F < 1$) or between the four change conditions [$F(3,30) = 2.2, p > 0.1$]. Subjects responded more quickly in the monitor-object task ($M = 507$ ms) than in the monitor-place task ($M = 574$ ms). Analysis of variance revealed that this difference was significant [$F(1,10) = 6.5, p < 0.05$], as were differences between the four change conditions [$F(3,30) = 6.9, p = 0.001$]. The latter effect was due to faster performance in the no-change condition ($M = 479$

ms) compared to the other three conditions ($M = 555$ ms for central object changes, 550 ms for peripheral object changes, 577 ms for place changes). As in the previous experiment, RTs did not differ significantly between the central object change, peripheral object change, and place change conditions (all $t_s < 1.2, n.s.$).

The fMRI results confirmed that the PPA response to different kinds of changes cannot be attributed solely to the location of those changes within the visual field (Figure 5). Indeed, there was a nonsignificant trend for the PPA to respond *less* strongly to objects in the periphery than it did to objects in the center of the visual field [$t(13) = 1.7, p = 0.11$]. As in Experiment 1, PPA response to the place changes was significantly greater than the response to central object changes [$t(13) = 2.17, p < 0.05$], and also significantly greater than the response to peripheral object changes [$t(13) = 3.08, p < 0.01$]. There were no significant differences between the three change conditions in LO (all $t_s < 1.4, all p_s > 0.19$) or in the FFA (all $t_s < 1$).

Figure 4 (right) illustrates the difference in response pattern between the three regions of interest. We observed a similar pattern to Experiment 1 with greater response in the PPA to place changes and greater response in LO to central object changes; however, in the present experiment, the region \times change-type interactions between the PPA and LO and between the PPA

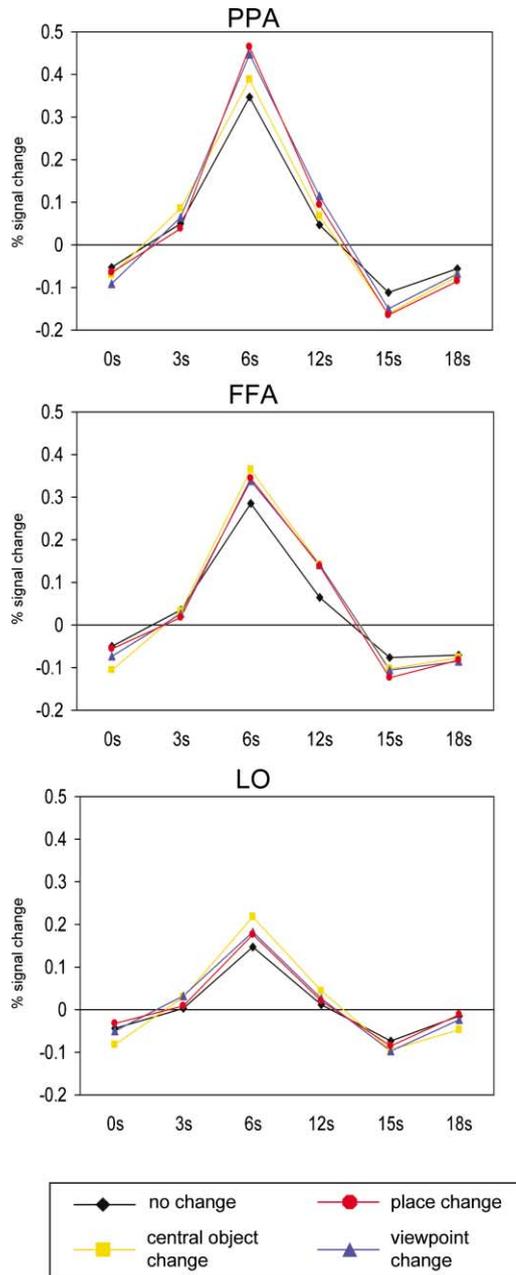


Figure 3. Results of Experiment 1
Event-related response to the four kinds of changes in the PPA, FFA, and LO (all right hemisphere) averaged over all subjects ($N = 15$) in Experiment 1. Responses to viewpoint and place changes are equal in the PPA, and greater than the response to object changes.

and FFA were only marginally significant [PPA versus LO, $F(2,18) = 2.63$, $p = 0.10$; PPA versus FFA, $F(2,22) = 2.87$, $p = 0.08$]. As before, there was no similar interaction between the FFA and LO ($F < 1$).

A comparison of the left and right panels of Figure 4 suggests that while the overall pattern of response was similar for Experiments 1 and 2, the differences between conditions were smaller in Experiment 2. For example, the difference between the place- and object-change conditions in the PPA was 0.8% in Experiment 1, but

only 0.3% in Experiment 2. Two differences might have led to this difference in the magnitude of response. First, the absence of the viewpoint-change condition in Experiment 2 might have prompted subjects to pay less attention to the spatial aspects of the scenes than they did in Experiment 1. Second, the inclusion of the peripheral object-change condition might have prompted subjects to analyze the scenes more as two-dimensional visual arrays than as depictions of three-dimensional spatial layouts because the objects were not integrated into the scene in this case. Indeed, the marginally greater PPA response in the central object-change compared to the peripheral object-change condition may reflect the fact that the changing object was a part of the three-dimensional scene in the former case but not the latter. Consequently, attention might have been drawn away from the spatial aspects of the scene more strongly in the peripheral object-change condition than in the central object-change condition.

In sum, Experiment 2 replicated the finding that the PPA responds more strongly to place changes than to object changes, and demonstrated that this differential response cannot be attributed solely to preferential processing of information from the periphery of the visual field.

Left Hemisphere Effects

In addition to the right hemisphere ROIs, a left-hemisphere PPA could also be defined for most subjects. Previous studies have suggested that left parahippocampal cortex might be less specialized than right parahippocampal cortex for spatial processing. For example, left but not right parahippocampal cortex has been implicated in verbal as well as visuospatial memory (Kirchhoff et al., 2000; Wagner et al., 1998). Nevertheless, the general pattern of response in the left PPA was similar to that of the right PPA, although less distinct (Figure 6). As in the right PPA, the response to viewpoint and place changes was equivalent [$t(12) = 1.2$, $p > 0.2$], although it here might be argued that there was a very slight nonsignificant trend toward greater response to the place changes. This trend is particularly interesting given that Vuilleumier et al. (2002) have recently reported evidence for viewpoint-independent object representations in left but not right fusiform gyrus. The response to place changes was significantly higher than the response to object changes [$t(12) = 3.5$, $p < 0.01$], but the greater response to viewpoint than to object changes did not reach statistical significance [$t(12) = 1.6$, $p > 0.1$]. There were no significant differences between the three change conditions in Experiment 2, although there was a trend toward greater response in the place-change condition when compared to the peripheral object-change condition [$t(12) = 1.81$, $p = 0.10$].

Task-Related Effects

The failure to observe effects of retinal eccentricity in Experiment 2 contrasts with the results of Levy et al. (2001), who reported differential activity in face- and house-selective areas corresponding to the FFA and PPA during viewing of centrally versus peripherally presented objects. One important difference between the two studies is that the Levy et al. study used a blocked

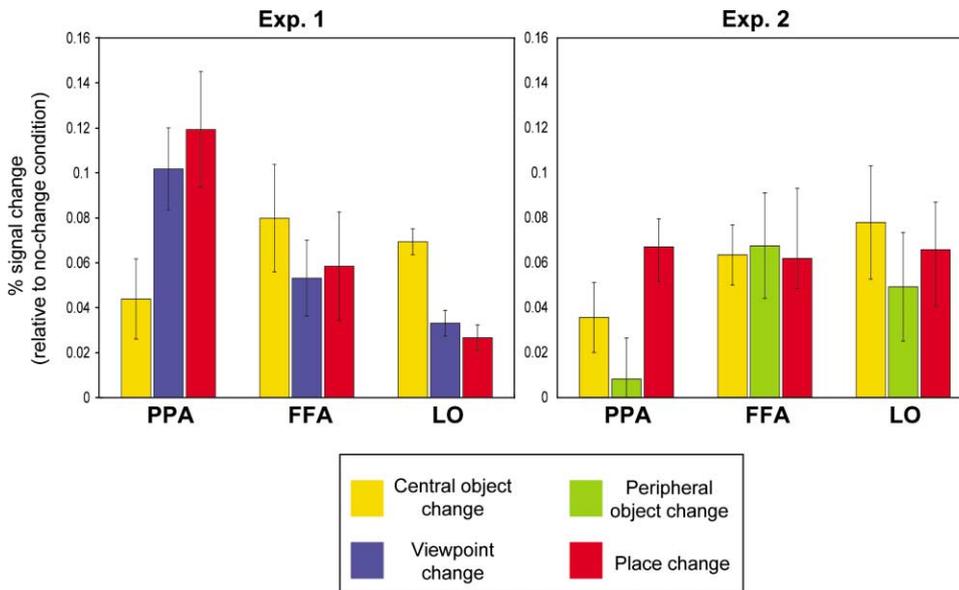


Figure 4. Comparison of Peak fMRI Response across Regions of Interest

Peak response to object, viewpoint, and place changes in the PPA, FFA, and LO in Experiment 1 (left), and for central object, peripheral object, and place changes in Experiment 2 (right). Values are plotted relative to the peak response in the no-change condition for each experiment. Error bars represent ± 1 SEM of this difference. Note that the PPA responds more strongly to place and viewpoint changes, while LO responds more strongly to object changes. PPA response to peripheral object changes is no greater than response to central object changes.

design in which response was measured over 18 s intervals of continuously presented central or peripheral objects, while we have used an event-related design. Previous studies have demonstrated that fMRI activity can be strongly modulated by attention (Wojciulik et al., 1998) even in the absence of any visual stimulus (Kastner et al., 1999). Thus, the eccentricity effects reported in the previous study might result from differential employment of attention to the center versus periphery rather than differential sensitivity to central versus peripheral visual information per se.

To examine this possibility, we compared the mean event-related response between the task blocks in both experiments. Subjects reported that they attended mostly to the center of the scene during the monitor-object blocks but attended to the whole scene during the monitor-place blocks. As the stimuli in both kinds of blocks were equivalent, we were able to observe block-related effects of central versus peripheral attention independent of differences in central versus peripheral visual stimulation. Results are shown in Figure 7. To increase the power available for this analysis, data from both experiments were combined, with experiment treated as a between-subject variable. No interactions of experiment and task difference were observed in any of the three regions (all $F_s < 1$).

Analysis of variance revealed greater response during the monitor-place task compared to the monitor-object task in the PPA [$F(1,26) = 23.5, p < 0.001$], and greater response to the monitor-object task compared to the monitor-place task in LO [$F(1,20) = 9.3, p < 0.01$]. No task-related differences were observed in the FFA ($F < 1$). These results can be interpreted in two possible ways: PPA and LO response might either be modulated

by tasks that require attention to spatial versus object information, or by tasks that require attention to the center versus periphery of the visual field. Although the present data do not allow us to decide between these two possibilities, the latter hypothesis would be consistent with the results of Levy et al., while the former hypothesis would not. Thus, the PPA and LO might be sensitive to manipulations that direct attention to either the center or periphery of the visual field, even though they are not sensitive to manipulation of central versus peripheral visual stimulation per se.

Interestingly, the task-related differences in the PPA and LO were at least partially uncoupled from stimulus presentation: *t* tests indicated that these differences were significant or nearly so at each time point in both the PPA (all $t_s > 3.4$, all $p_s < 0.002$) and LO (all $t_s > 2.1$, all $p_s < 0.051$), including the first time point (prior to any hemodynamic response due to stimulus presentation) and the last time point (when stimulus-related response should have returned to baseline). The interaction between task-related differences and time was significant in the PPA [$F(5,130) = 6.4, p < 0.001$] but not LO ($p > 0.3$). This pattern might be due to a block-related baseline shift effect. However, it could also result from temporal overlap between adjacent trials within a task block. The present data do not allow us to distinguish between these two possibilities.

Discussion

The aim of this study was to determine whether scene representations in the parahippocampal place area are viewpoint specific or viewpoint invariant. The results demonstrate that they are viewpoint specific: the PPA

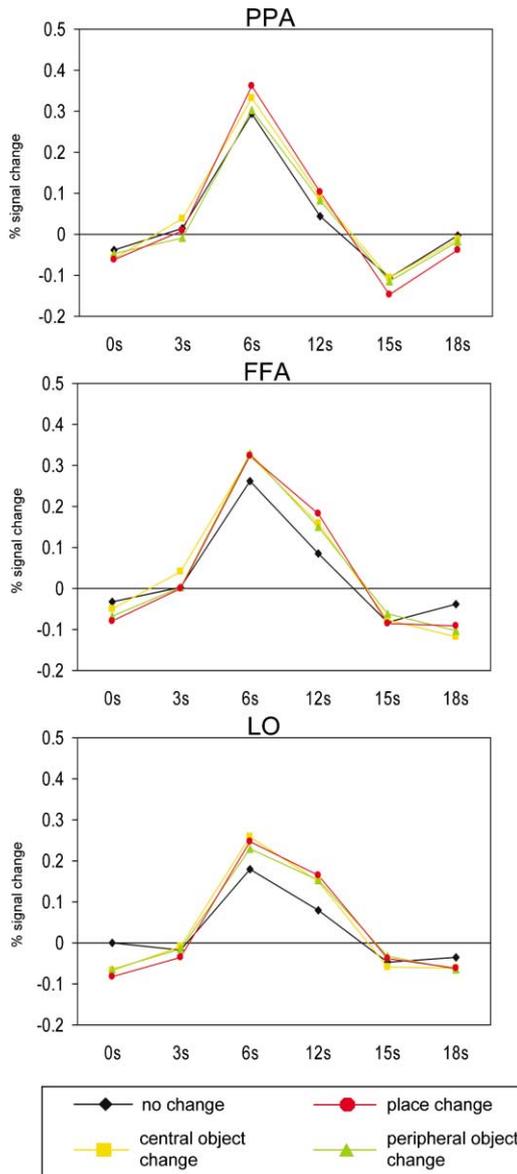


Figure 5. Results of Experiment 2
Event-related response to the four kinds of changes in the PPA, FFA, and LO (all right hemisphere) averaged over all subjects (N = 14) in Experiment 2.

responds just as strongly to changes in viewpoint as it does to changes in scene layout and more strongly to both of these changes than to object changes. As far as the PPA is concerned, two views of the same scene are as representationally distinct as two views of entirely different scenes.

Previous work has implicated parahippocampal cortex in processing information about the spatial structure of visual scenes (Epstein et al., 1999; Epstein and Kanwisher, 1998). The present results confirm this hypothesis by demonstrating that the PPA responds much more strongly to events in which the spatial relationship between the observer and the scene changes than it does to equally salient events in which a prominent object within the scene changes but the overall spatial frame-

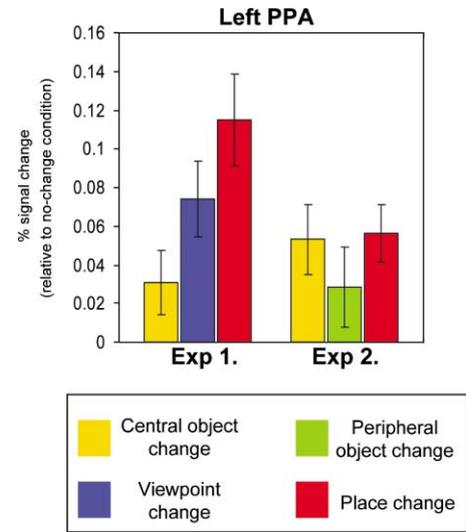


Figure 6. Response in left PPA
Peak response to object, viewpoint, and place changes in the left hemisphere PPA plotted relative to the peak response in the no-change condition for Experiment 1 (left) and Experiment 2 (right). Error bars represent ± 1 SEM of this difference.

work remains constant. Importantly, these results cannot be explained by assuming that the place and viewpoint changes are generally more salient than the object changes, because the opposite pattern (greater response to object than to place or viewpoint changes) was observed in LO.

What do the current results tell us about the PPA's role in spatial processing and navigation? At least one scenario can be questioned: the PPA does not appear to represent the geometry of the scene in an intrinsic (i.e., scene-centered) coordinate frame. Rather, it represents the spatial relationship between the observer and the set of connected surfaces that defines the scene. Such a representation would be a necessary precursor to any computation of the location and orientation of the body relative to an internal map of the world. Neurophysiological data indicate that the latter kind of information is represented by distinct groups of cells in the rat. In particular, location in the world is encoded by place cells in the hippocampus (Best et al., 2001; O'Keefe and Nadel, 1978), while orientation is encoded by head direction (HD) cells in the postsubiculum, retrosplenial cortex, and other limbic regions (Muller et al., 1996; Taube, 1998). Although combined lesion/recording studies have demonstrated that the location and orientation representations supported by these two sets of cells are not strictly dependent on each other (Golob and Taube, 1997), they are tightly coupled in most circumstances (Knierim et al., 1995), and both are strongly controlled by the geometric configuration of visible landmarks or barriers (O'Keefe and Speakman, 1987; Taube, 1998). These results suggest that both place cells and head direction cells may receive common input from a representation of the relationship between the geometric structure of the visible environment and the observer. The PPA may be the locus of this representation in humans.

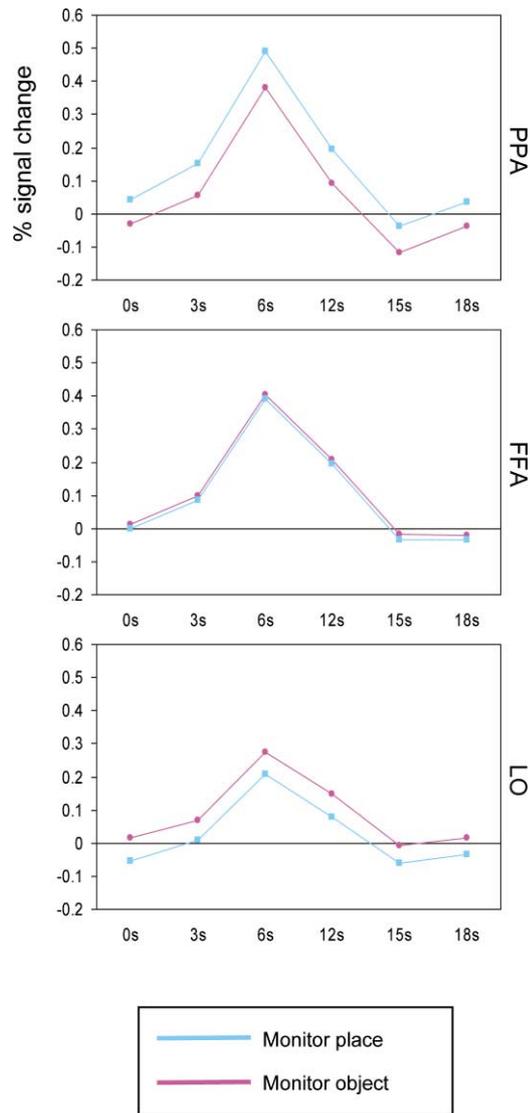


Figure 7. Effect of Task in the PPA, FFA, and LO

The mean event-related response during monitor-object and monitor-place blocks is shown (averaged over all subjects in both experiments). The level of activity in the PPA is significantly higher when subjects attend to the entire scene (monitor-place task) than when they attend to the central object (monitor-object task), while the opposite pattern is observed in LO. No task-related differences were found in the FFA.

The finding of viewpoint-specific scene representations in the PPA is in line with behavioral studies that indicate that objects are also represented in a viewpoint-dependent manner (Tarr et al., 1998; Bulthoff et al., 1995; Williams and Tarr, 1999). Despite these findings, some researchers have argued for viewpoint-independent object representations (Biederman and Gerhardstein, 1993), and the issue remains controversial (e.g., Bar, 2001; Biederman and Bar, 1999; Hayward and Tarr, 2000; Tarr and Bulthoff, 1995). Interestingly, some recent neurophysiological and neuroimaging data suggests that viewpoint-dependent and viewpoint-independent object representations may coexist (Burgund and Marsolek, 2000; Vuilleumier et al., 2002). For example, Booth and Rolls (1998) observed that while the majority of

neurons in monkey inferior temporal cortex responded to specific views of objects, a small subset responded in a viewpoint-invariant manner. Insofar as fMRI measures the average response within a region rather than the response to individual neurons, the present results do not preclude a similar scenario in which a small number of neurons in the PPA might represent scenes in a viewpoint-invariant manner; however, they do suggest that the majority of PPA cells are viewpoint dependent.

The present results are also consistent with behavioral studies that have demonstrated viewpoint-dependent encoding of object locations. When subjects view scenes consisting of objects arrayed on a tabletop or within a room, their subsequent memory for the arrangement of the objects is most accurate if they are tested using identical or similar views (Diwadkar and McNamara, 1997; Shelton and McNamara, 1997), indicating a cost for extrapolating to unfamiliar views. Insofar as the PPA does not appear to process information about individual objects, this behavioral effect is unlikely to be directly attributable to viewpoint-dependent encoding in the PPA. Indeed, neuroimaging studies that have examined memory for object locations (albeit in two-dimensional rather than three-dimensional arrays) have activated parietal cortex (Kohler et al., 1995; Owen et al., 1996a) and entorhinal cortex (Johnsrude et al., 1999; Owen et al., 1996b) rather than the PPA (but see Maguire et al., 1998b). Furthermore, behavioral data suggest that representations of object location and environmental geometry might be dissociable: Wang and Spelke (2000) reported that memory for the arrangement of the corners of a room survived a disorientation procedure that eliminated memories for the locations of individual objects. However, there is also data indicating a high degree of interaction between these two kinds of spatial representations. For example, Shelton and McNamara (2001) found that views of an object array were much more likely to be encoded when they were aligned with the surrounding room than when they were misaligned (see also Mou and McNamara, 2002), while Simons and Wang (1998; Wang and Simons, 1999) observed that the cost of extrapolating to an unfamiliar view was smaller when the subject moved relative to the array (and, consequently, relative to the environment) than when the object array was rotated but the observer remained stationary. These results suggest that viewpoint-specific representations of the layout of the surrounding environment supported by the PPA might play a key role in guiding the formation of viewpoint-dependent memories for the locations of individual objects.

One caveat to the above claims about viewpoint dependence is the fact that the present study only examined adaptation effects between stimuli that were unfamiliar to the subject at the beginning of the experiment. Some evidence suggests that cortical representations reorganize themselves over periods of days and weeks to reflect relationships between stimuli that often appear together (Erickson et al., 2000; Sakai and Miyashita, 1991). In the real world, different views of the same place cooccur frequently, while views of different places almost never cooccur. Thus, it is possible that consolidation processes operating over time periods longer than the length of this experiment might lead to the formation of links between viewpoint-specific representations corresponding to the same "place" in the world.

In this way, the PPA might come to represent familiar places in a partially viewpoint-independent manner. This process might be aided by the encoding of information about spatial transitions between different viewpoints that would be attainable in the real world through active navigation but was not available in the present experiment. Alternatively, viewpoint-independent scene representations might be supported by other cortical regions such as the hippocampus (Burgess et al., 2001; Georges-Francois et al., 1999; King et al., 2002; Maguire et al., 1998a). Future studies will examine these hypotheses.

In addition to the main findings demonstrating viewpoint dependence in PPA response, the current experiments replicated earlier results that indicated that the response of the PPA and LO can be modulated by tasks that require attention to either the center or periphery of the visual field (Hasson et al., 2002; Levy et al., 2001). The previous experiments used a blocked design that did not allow effects of central versus peripheral visual stimulation to be distinguished from effects of central versus peripheral visual attention. Experiment 2 suggests that these regions are not sensitive to effects of central versus peripheral visual stimulation *per se*. Rather, in both experiments there was a strong task-related effect that may relate to the different attentional demands of the two tasks. The precise nature of the relationship between these task-related effects and stimulus-related effects merits further investigation.

Finally, the current results have implications for our understanding of the functional organization of the ventral visual stream. It has recently been argued that ventral temporal cortex supports a distributed object form map that distinguishes between different kinds of objects on the basis of their pattern of induced cortical activation (Haxby et al., 2001; Ishai et al., 1999; but see Spiridon and Kanwisher, 2002). Insofar as the current experiments measured cortical response only in three regions of peak selectivity to certain stimulus categories, they do not speak to the issue of whether these regions are distinct and modular or part of a larger distributed map. However, they do suggest that the “objects” represented in ventral temporal cortex include more than just discrete convex objects such as shoes and bottles. Indeed, we propose that the functional organization of ventral temporal cortex might reflect its role in processing fundamentally different kinds of information available within visual scenes. In particular, the PPA might process information about the relationship between the observer and the overall spatial structure of the scene (as conveyed by large surfaces that “enclose” the observer such as walls, hills, and the sides of buildings), LO might process information about the shapes of (potentially movable) objects in the scene, and specialized modules such as the FFA and the Extrastriate Body Area (EBA; Downing et al., 2001) might be dedicated to analyses that can only be performed on certain object categories such as faces or bodies.

Experimental Procedures

Subjects

Fifteen volunteers (5 females; mean age 25.3 ± 5.4 years) were recruited from the greater Oxford community for Experiment 1, and 14 different volunteers (6 females; mean age 22.3 ± 3.0 years) for

Experiment 2. All subjects were right-handed and had normal or corrected to normal vision. Ethical approval for the study was obtained from the Central Oxford Research Ethics Committee.

fMRI Parameters

Scanning was carried out at the Functional Magnetic Resonance Imaging of the Brain (fMRIB) Centre, Oxford, UK on a 3 Tesla MRI system driven by a Varian Unity Inova console and equipped with an Oxford Magnet Technology magnet, a Siemens body gradient coil and a bird-cage radio-frequency head coil. T2*-weighted images were acquired using a gradient echo echoplanar pulse sequence (TR = 3s, TE = 30 ms, flip angle = 90°, matrix size = 64×64 , FOV = 192×256 mm) sensitive to blood oxygen level-dependent (BOLD) contrast. Each functional volume consisted of 21 contiguous 6 mm axial slices.

Procedure

Scanning sessions consisted of two experimental scans followed by two localizer scans (Experiments 1 and 2), followed by a control scan (Experiment 2 only).

Experimental scans were 11 min and 36 s long and were divided into four equal length blocks. Each block began with a 6 s presentation of an instruction screen that indicated which of the two tasks was to be performed during the block, followed by a fixation dot for 9 s. This was followed by 36 4-second-long trials, 24 of which were stimulus trials and 12 were “null” trials. Stimulus trials consisted of a 350 msec prestimulus interval followed by the sequential presentation of two scenes for 300 msec each separated by a blank 100 msec interval, followed by a 2950 msec poststimulus period, during which subjects made their response using a button box. The fixation dot remained on the screen throughout the trial except when the scenes were on the screen and during the interscene interval. During null trials, the fixation dot remained on the screen for 4 s and subjects made no response. Each block ended with a 15 s fixation period.

Stimuli in Experiment 1 were 80 photographs of tabletop or partial room scenes. Each scene contained a large prominent central object, which was displayed in color to enhance its distinction from the grayscale background. The 80 photographs were organized into 20 sets of 4 images, corresponding to four types of changes within a scene. Each set of four included photographs of (1) a base scene, (2) the same scene from a different viewing angle, (3) the same scene with a different central object, and (4) a different scene consisting of the same central object as the base scene but in different surroundings. The first of the two photographs presented in each stimulus trial was always the base scene, and the second was either the exact same photograph (no-change trials) or one of the three other photographs from the same set depending on trial type (viewpoint-change, object-change, or place-change trials). There were six trials for each of the four trial types in each block. Order of trial presentation was randomized separately for each block subject to the constraint that trials of every type were preceded equally often by trials of every other type (including trials of the same type).

Experiment 2 was identical to Experiment 1 in the no-change, object-change, and the place-change conditions. The fourth condition in this experiment was the periphery-change condition, which replaced the viewpoint-change condition of Experiment 1. In this condition, the second photograph of each event was identical to the first photograph except for two identical grayscale objects overlaid in opposite corners (Figure 1). These objects were copied directly from the images used in the object-change trials using Adobe Photoshop.

Subjects performed one of two possible tasks during each block. In monitor-object blocks, they used a button box to indicate whether the central object differed between the two photographs in a trial (i.e., object-change trials) or remained the same (i.e., no-change, viewpoint-change, place-change, or periphery-change trials). In monitor-place blocks, they indicated whether the overall spatial context differed between the two photographs (i.e., place-change trials) or remained the same (i.e., no-change, object-change, viewpoint-change, or periphery-change trials). Task blocks alternated within a scan in an ABAB fashion, and the order was counterbalanced across scans and across subjects. Stimuli were projected onto a screen located at the foot end of the scanner bed, which

was viewed through prism spectacles, and subtended a visual angle of approximately 11.8°.

In localizer scans, subjects viewed digitized grayscale photographs of faces, common objects, indoor scenes, and two other object categories designed to test other hypotheses not discussed here. Each scan was 6 min and 15 s long and was divided into 20 15 s picture epochs (four for each of the stimulus categories) interleaved with five epochs during which the screen was blank except for fixation point. During each picture epoch, 20 different photographs of the same type were shown. Each photograph was presented for 300 msec followed by a blank interval of 450 msec. Epoch order was counterbalanced as described previously (Epstein et al., 1999; Epstein and Kanwisher, 1998). Subjects performed a one-back task in which they were required to press a button whenever two identical stimuli appeared in a row.

fMRI Data Analysis

Functional images were preprocessed using SPM99 (Wellcome Department of Cognitive Neurology, London). Images were corrected for differences in slice timing by resampling slices in time to match the first slice of each volume. For each subject, images were then realigned with respect to the first image using sinc interpolation. The mean realigned image was then normalized to an EPI template in Montreal Neurological Institute (MNI) space using affine and smoothly nonlinear transformations. For this transformation, a masked normalization procedure was used to prevent mismatch caused by signal dropout artifact in the mean image (Brett et al., 2001). This transformation was then separately applied to all functional images for the subject. Images were then resampled into 2 mm isotropic voxels and spatially smoothed with an 8 mm FWHM Gaussian filter.

Regions of interest were defined individually for each subject using data from the localizer scans, which were analyzed using a general linear model as implemented in SPM99. For each scan, the response at each voxel was modeled using an 11-regressor model in which the first five regressors modeled the response to each of the five stimulus types as a boxcar function convolved with a canonical hemodynamic response function, and the next six regressors modeled motion-specific effects. Data was temporally filtered before analysis to remove low-frequency confounds. Linear contrasts were used to identify clusters of contiguous voxels in the occipital temporal region that responded significantly more ($p < 0.05$, corrected for multiple comparisons) to (1) scenes compared to objects (candidate PPA voxels), (2) faces compared to objects (candidate FFA voxels), and (3) objects compared to scenes (candidate LO voxels). As we wished to distinguish between the functional response in regions that were spatially very proximate, we used a particularly stringent definition of the PPA, FFA, and LO, which we defined for each subject by identifying the most significant voxel in each of these clusters. When a cluster had more than one peak voxel, the coordinates of both were used to define the region of interest. Using this criterion, PPA and FFA could be identified in the right hemisphere in 14 out of 15 subjects and LO in 12 of 15 subjects in Experiment 1. Mean Talairach coordinates were PPA = (28, -46, -10), FFA = (44, -51, -25), LO = (48, -68, -11). For Experiment 2, the PPA was identified in the right hemisphere in all 14 subjects, the FFA in 12 out of 14 subjects, and LO in 10 out of 14 subjects. Mean Talairach coordinates were PPA = (29, -43, -11), FFA = (44, -53, -23), LO = (50, -67, -10). The location of these regions of interest was highly consistent across subjects and experiments (see Figure 2). In addition, the PPA could be identified in the left hemisphere in 13 out of 15 subjects in Experiment 1 and 13 out of 14 subjects in Experiment 2. Mean Talairach coordinates were (-26, -48, -9) for Experiment 1 and (-28, -47, -10) for Experiment 2.

The time course of activation during the experimental scans was then extracted for each of the ROIs for each subject. Note that because of spatial smoothing, each peak voxel translates into a 8-mm-wide FWHM Gaussian ROI. This data was then temporally filtered to remove temporal components with a period of longer than 50 s. (For the task-related analyses, the data were refiltered to remove only components with a period of longer than 700 s, thus ensuring that block-related components were not removed.) The event-related response for each trial was extracted and the mean

response for each trial type was calculated for each subject. For trials in which the trial start time did not correspond precisely to a MR acquisition, an equivalent response time course was calculated by taking the weighted average of the preceding and succeeding MR response level for each time point. For example, if a trial began at $(t - 1)$ s, then the first point of the time course was calculated by $0.667 \cdot R(t - 1) + 0.333 \cdot R(t + 2)$, where $R(t - 1)$ is the level of response at $(t - 1)$ s and $R(t + 2)$ is the level of response in the next MRI acquisition 3 s later.

Control Experiment

In both experiments, the photographs presented first in each event were drawn from the same set for all four conditions, but the photographs presented second were drawn from different sets for each condition. Thus, it is theoretically possible that differences between conditions are due to stimulus differences between the four photograph sets rather than differences in the relationship between the first and second image. To examine this possibility, subjects in Experiment 2 were run on a one scan of a control experiment in which only one photograph was shown in each trial. Photographs were shown for 300 msec and were preceded by a 350 msec prestimulus interval and followed by a 3250 msec poststimulus period, during which subjects responded by pressing a button to indicate that the stimulus had been seen. Stimuli were the same scenes that had been presented as the second items in Experiment 2, and the overall design was otherwise the same. Thus, this experiment allowed us to examine the event-related response to the different stimulus sets used in Experiment 2 in a situation where the stimuli did not appear in the context of an immediately preceding item. No differences in response between the stimulus sets was found in either the PPA (all $t_s < 1$), FFA (all $t_s < 1.9$, all $p_s > 0.05$), or LO (all $t_s < 1.7$, all $p_s > 0.1$). Thus, differences between the stimulus sets are unlikely to explain the present results.

Pilot Experiment

In order to establish the efficacy of tabletop scenes for activating the PPA, five subjects were run in a pilot experiment in which they viewed color photographs of tabletop scenes, landscapes, and common objects (as well as other stimuli) in a blocked design. Stimuli were presented in 16 s blocks, with each photograph on the screen for 300 msec and a 500 msec ISI. In half of the scans, stimuli were passively viewed. In the other half of the scans, subjects performed a one-back repetition detection task in which they were required to press a key whenever the same stimulus appears twice in succession. Repetitions occurred twice in each block. The PPA was defined using an independent localizer scan as described above. Data from the left and right hemisphere were combined. Subjects were tested on a 4T scanner at the University of Western Ontario, using a custom surface coil. The mean percent signal change in the PPA relative to a fixation baseline was 1.4% for tabletop scenes and 1.3% for landscapes. This difference was not significant [$t(4) = 1.25$, n.s.]. The response to objects (0.5%) was significantly lower than the response to both tabletop scenes [$t(4) = 4.85$, $p < 0.01$] and to landscapes [$t(4) = 5.5$, $p < 0.01$]. Thus, the PPA responds just as strongly to tabletop scenes as to environmental scenes, which have been previously shown to maximally activate this region.

Acknowledgments

We thank Nancy Kanwisher and John Duncan for helpful discussions of these results and Peter Hobden, Paul Matthews, and the staff of the Oxford Centre for Functional Magnetic Resonance Imaging of the Brain for assistance with data collection. This research was supported by the UK Medical Research Council.

Received: August 5, 2002

Revised: January 9, 2003

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