

Position Selectivity in Scene- and Object-Responsive Occipitotemporal Regions

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MacEvoy SP, Epstein RA. Position selectivity in scene- and object-responsive occipitotemporal regions. *J Neurophysiol* 98: 2089–2098, 2007. First published July 25, 2007; doi:10.1152/jn.00438.2007. Complex visual scenes preferentially activate several areas of the human brain, including the parahippocampal place area (PPA), the retrosplenial complex (RSC), and the transverse occipital sulcus (TOS). The sensitivity of neurons in these regions to the retinal position of stimuli is unknown, but could provide insight into their roles in scene perception and navigation. To address this issue, we used functional magnetic resonance imaging (fMRI) to measure neural responses evoked by sequences of scenes and objects confined to either the left or right visual hemifields. We also measured the level of adaptation produced when stimuli were either presented first in one hemifield and then repeated in the opposite hemifield or repeated in the same hemifield. Although overall responses in the PPA, RSC, and TOS tended to be higher for contralateral stimuli than for ipsilateral stimuli, all three regions exhibited position-invariant adaptation, insofar as the magnitude of adaptation did not depend on whether stimuli were repeated in the same or opposite hemifields. In contrast, object-selective regions showed significantly greater adaptation when objects were repeated in the same hemifield. These results suggest that neuronal receptive fields (RFs) in scene-selective regions span the vertical meridian, whereas RFs in object-selective regions do not. The PPA, RSC, and TOS may support scene perception and navigation by maintaining stable representations of large-scale features of the visual environment that are insensitive to the shifts in retinal stimulation that occur frequently during natural vision.

INTRODUCTION

Neurons in the visual system commonly respond to stimuli falling in a limited region of the visual field. Since Hartline (1938), the spatially specific receptive field (RF) has been considered a central organizing feature of the visual system and, over the past four decades, explorations of mammalian visual areas have usually begun by characterizing the general sizes and spatial arrangements of their constituent neurons' RFs. At the same time, however, the spatial specificity of individual units is seemingly at odds with the visual system's task of guiding behaviors that are specific for the identities of objects and environments we encounter, irrespective of their immediate appearance. For instance, as a consequence of our movement through the world, the movements of objects within it, and gaze shifts, patterns of light reflected by objects onto the retina change frequently and often unpredictably. Given the spatial specificity of RFs throughout the visual system, this means that the pattern of neural activity evoked by a single object can vary widely as well. In spite of these variations,

however, the visual system ultimately must extract the identities of objects in an invariant manner.

Recognizing this tension, many authors have concluded that information about object identity must ultimately be encoded by neurons high in the visual hierarchy that respond to the presence of a specific object in a manner that is completely invariant with respect to retinotopic position, a role that has been suggested for neurons of the anterior inferotemporal cortex (IT) (Logothetis and Sheinberg 1996; Tanaka 1996). In macaques, IT neurons are well known to be selective for highly complex shapes such as objects and faces, and early studies suggested they possessed remarkable tolerance for position changes and far larger RFs than found in earlier visual areas (Boussaoud et al. 1991; Gross et al. 1972; Tovee et al. 1993). More recent work, however, argues against the idea of a position-invariant representation of objects in IT. Although neurons in IT respond to their preferred stimuli over a wider area than neurons in earlier visual areas, mounting evidence demonstrates that IT neurons can encode precise information about the positions of objects in the visual field (Aggelopoulos and Rolls 2005; DiCarlo and Maunsell 2003). In humans, functional magnetic resonance imaging (fMRI) studies (Larsson and Heeger 2006; McKyton and Zohary 2007; Niemeier et al. 2005) and subdural electrode recordings (Yoshor et al. 2006) indicate similar position selectivity in the object-selective lateral occipital complex (LOC), a large region thought to be the human homologue of IT.

In addition to processing information about individual, discrete objects, our visual system appears to extract information about the overall ambient scene, treating the scene as a kind of object in its own right (Epstein 2005; Henderson and Hollingworth 1999; Introub 1997). fMRI studies have identified several regions of the human brain that are more active when subjects view complex visual scenes such as landscapes, cityscapes, or rooms than when they view individual discrete objects such as faces, tools, or appliances. These regions include the parahippocampal place area (PPA) within posterior parahippocampal cortex (Aguirre et al. 1998; Epstein and Kanwisher 1998; Epstein et al. 1999; Ishai et al. 1999), the retrosplenial cortex/parietal-occipital sulcus region (RSC) (Maguire 2001), and a region near the transverse occipital sulcus (TOS) (Grill-Spector 2003; Hasson et al. 2003; Nakamura et al. 2000). Neuropsychological and neuroimaging studies suggest that these scene-responsive regions mediate place recognition and other functions that are critical to our ability to accurately navigate through the world (Aguirre and D'Esposito

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1999; Epstein 2005; Maguire et al. 1998; Mendez and Cherrier 2003). Nonetheless, little is known about the basic response properties of the neurons in these regions or about the precise contribution each region makes to scene perception and navigation.

As in object-selective cortex, understanding the position specificity of neurons in scene-selective regions could help elucidate their functions. For example, if these regions contain neurons with RF sizes similar to LOC, this may indicate that they encode local features common to environmental scenes such as doors, windows, bricks, and tree trunks. On the other hand, if these regions contain neurons with larger, less position-specific RFs, this may indicate that they encode information about more global visual features that are truly unique to scenes, such as large extended surfaces defined by walls, hillsides, and other topographical features, which can be identified only by integrating visual information over large portions of the visual field.

In the absence of identified functionally homologous structures in the macaque, previous studies provide limited insight into these issues. Among the few studies addressing the topography of scene-selective regions, Levy et al. (2001, 2004) demonstrated that the PPA and TOS are particularly sensitive to stimuli falling in the visual periphery. Although this finding is consistent with the broad sensitivity one would expect from position-invariant neurons, smaller position-selective RFs could have produced the same result. Indeed, given the complementary preference of human object-selective regions for central stimulation, the results of Levy et al. could be taken to indicate that the PPA is nothing more than object-selective cortex for the visual periphery, its preference for scenes a simple consequence of the tendency of scenes to encompass greater portions of visual space than objects.

To test the level of position specificity among neurons in human scene-selective regions, we adopted an fMRI-adaptation (fMRI-a) approach previously developed by McKyton and Zohary (2007) to examine visuotopy in the object-selective lateral occipital complex (LOC). Like other fMRI-a designs (Grill-Spector and Malach 2001; Kourtzi and Kanwisher 2001), this paradigm takes advantage of the reduction in hemodynamic response to repeated stimuli. When sequential stimuli differ in a way that relieves this adaptation, we may infer that they activate different neural populations, even when those populations cannot be directly resolved by MR signals. By extension, we may conclude that neurons in these regions encode the variable that distinguishes the stimuli from each other.

More specifically, we reasoned that position-invariant scene-selective regions should exhibit adaptation to repeated scenes and that the magnitude of this adaptation should not depend on whether the scene was previously presented in the same visual hemifield or in the opposite visual hemifield. Conversely, we reasoned that regions possessing visuotopic specificity would exhibit significantly less adaptation when scenes were presented in opposite hemifields than when they appeared at the same visual hemifield. To make a fair comparison to previous studies, we also used object stimuli to examine position specificity in LOC.

To anticipate, we found that adaptation effects in scene-selective regions, particularly in the PPA and RSC, were minimally sensitive to stimulus position. In contrast, adaptation

in LOC was strongly position selective, consistent with previous work. Taken together, these results suggest that neurons in scene-selective regions possess larger RFs than those found in object-selective cortex, and that they may contribute to scene perception and navigation by maintaining a representation of the visual environment that is invariant to the retinal position of stimuli.

METHODS

Subjects

Ten subjects (seven female, aged 19–25 yr) with normal or corrected-to-normal vision were recruited from the University of Pennsylvania community and gave written informed consent in compliance with procedures approved by the University of Pennsylvania institutional review board. Subjects were paid for their participation. An additional subject was also scanned, but was excluded from the study before data analysis because of excessive head motion.

MRI acquisition

Scans were performed at the Center for Functional Neuroimaging at the University of Pennsylvania on a 3T Siemens Trio scanner equipped with a Siemens body coil and an eight-channel multiple-array Nova Medical head coil. Structural T1*-weighted images for anatomical localization were acquired using a 3D MPRAGE pulse sequences [repetition time (TR) = 1,620 ms, echo time (TE) = 3 ms, inversion time (TI) = 950 ms, voxel size = $0.9766 \times 0.9766 \times 1$ mm, matrix size = $192 \times 256 \times 160$]. T2*-weighted scans sensitive to blood oxygenation level-dependent (BOLD) contrasts were acquired using a gradient-echo echo-planar pulse sequence (TR = 3,000 ms, TE = 30 ms, voxel size = $3 \times 3 \times 3$ mm, matrix size = $64 \times 64 \times 45$).

Stimuli

Stimuli in scene experiments were 192 photographic images of unfamiliar indoor and outdoor scenes, including some from the McGill Calibrated Color Image Database (<http://tabby.vision.mcgill.ca>) (Olmos and Kingdom 2004). All images were cropped to 410×480 pixels. For object experiments, stimuli consisted of 192 computer-rendered images of common objects centered on a gray field with the same dimensions as the scenes. Each scene and object image subtended $9.16 \times 10.85^\circ$. Visual stimuli were rear-projected onto a Mylar screen at the head end of the scanner bore with an Epson 8100 3-LCD projector equipped with a Buhl long-throw lens and viewed through a mirror affixed to the head coil. The entire projected field subtended $22.9 \times 17.4^\circ$ and was viewed at $1,024 \times 768$ -pixel resolution.

Procedure

The scanning session for each subject consisted of eight experimental scans and two functional localizer scans.

Experimental scans were 6 min 51 s in length, and were divided into 16 12-s blocks separated by 12-s intervals, with additional 15- and 12-s fixation periods at the beginning and end of each scan, respectively. Following the design of McKyton and Zohary (2007), blocks were divided into four types that we termed Fixed-Novel, Fixed-Repeat, Cross-Novel, and Cross-Repeat (Fig. 1). Four blocks of each type were presented in each scan.

In Fixed-Novel blocks, subjects were required to initially fixate a central target for 500 ms and then maintain fixation while a sequence of 12 images was presented at a single location centered 5.725° to one side of the fixation target. On half of the blocks this location was to the left of the fixation target and for the other half it was to the right.

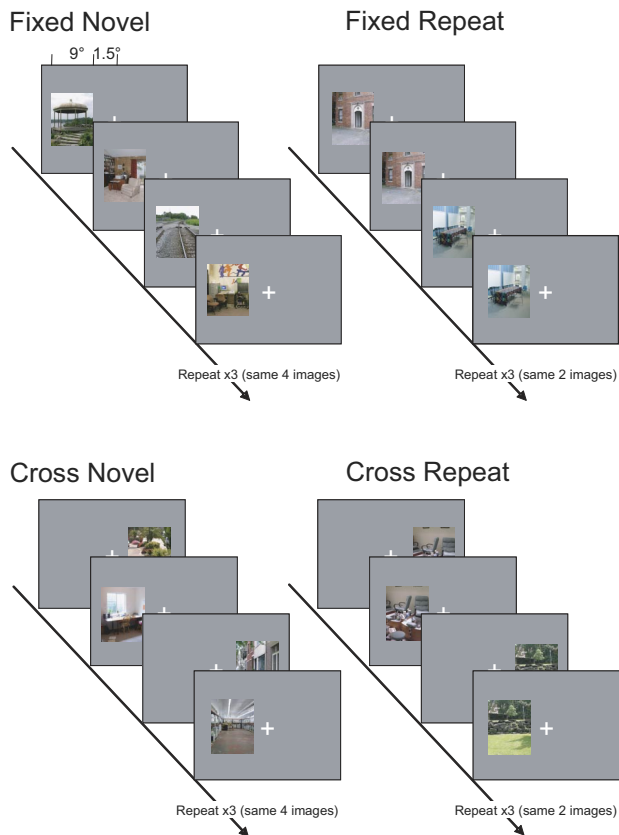


FIG. 1. Experimental design. Subjects were asked to fixate a central cross while stimuli (scenes or decontextualized objects) appeared either to the left or the right of fixation. Blocks began with a 500-ms fixation period. Individual images appeared for 775 ms, separated by 200-ms fixation-only intervals. As illustrated, images were not repeated across blocks: for each subject, a given image was seen in only a single block.

Stimuli (either scenes or objects, depending on scan) were a sequence of four unique images repeated three times (A–B–C–D–A–B–. . .). Each image was presented for 775 ms, followed by a 200-ms fixation-only period before the next image appeared.

In Fixed-Repeat blocks, the 12 stimuli were composed of two different images presented as six alternating same-image pairs (A–A–B–B–A–A–. . .). Again, stimuli were presented in the left hemifield on half the blocks and in the right hemifield in the other half.

Cross-Novel blocks were identical to Fixed-Novel blocks, except stimuli alternated between the left and right stimulus positions. Similarly, stimuli in Cross-Repeat blocks followed the same order as Fixed-Repeat, but with alternating stimuli appearing in opposite hemifields. For half of the Cross-Novel and Cross-Repeat blocks the first stimulus appeared on the left and in the other half the first stimulus appeared on the right. For each hemifield, Cross-Novel and Cross-Repeat blocks provided identical stimulation: two alternating stimuli (Fig. 1). Thus any difference between Cross-Novel and Cross-Repeat can be attributed unambiguously to cross-hemifield adaptation.

Stimuli were scenes in four scans and decontextualized objects in the other four scans. Thus in each scanning session there were a total of 64 scene blocks and 64 object blocks. Each block used a unique set of stimuli, so no image appeared in more than one block. This was done to ensure that no cross-block adaptation effects developed between Novel and Repeat blocks that might have confounded comparisons of Fixed and Cross adaptation.

To ensure that subjects attended to scenes, subjects were asked to detect blurry spots that appeared during the last 100 ms of randomly selected images in each block, without diverting their gaze from the fixation target. Blurry spots consisted of a randomly positioned

100-pixel-diameter circular window within which the image was convolved with a 10-pixel Gaussian filter. The number of blurry spots within each block ranged from two and six, and spots appeared in 25% of stimuli on average. (Note that this percentage applied to the total number of stimuli, of which there were 12 per block, and not the number of unique images, which was either two or four per block. Also, the appearance of a blurry spot during one presentation of an image did not necessarily mean that it would appear at the same location, nor at all, when that image was presented again.) Subjects were asked to signal by button press as soon as possible after a blurry spot was detected. In object runs, subjects were asked to silently name each object as it appeared, replicating the procedure of McKyton and Zohary.

Functional localizer scans were 8 min 15 s long and were divided into 15-s picture epochs during which subjects viewed color photographs of scenes, common objects, and phase-scrambled objects presented at a rate of 1.33 pictures/s in a blocked design as described previously (Epstein and Higgins 2007).

Data analysis

Functional images were corrected for differences in slice timing by resampling slices in time to match the first slice of each volume, realigned with respect to the first image of the scan, spatially normalized to the Montreal Neurological Institute (MNI) template, and spatially smoothed with an 8-mm FWHM (full width at half-maximum) Gaussian filter. Data were analyzed using the general linear model as implemented in VoxBo (www.voxbo.org) including an empirically derived 1/f noise model, filters that removed high and low temporal frequencies, regressors to account for global signal variations, and nuisance regressors to account for between-scan differences.

Functional regions of interest (ROIs) were defined for each subject using data from the functional localizer scans. These regions consisted of voxels responding more strongly ($t > 3.5$) to scenes than to common objects in the posterior parahippocampal/collateral sulcus region (PPA), retrosplenial cortex/parietal-occipital sulcus (RSC), and transverse occipital sulcus (TOS). Using these criteria, we identified both the left and right PPA in all subjects. For two subjects we were unable to identify left RSC and for another we could not identify the left TOS. For one additional subject neither left nor right TOS was identified. We also identified voxels corresponding to the lateral occipital complex (LOC) by stronger responses ($t > 3.5$) to objects than to scrambled objects. LOC was identified in all subjects. The time course of MR response during the main experimental scans was extracted from each ROI (averaging over all voxels) and entered into the general linear models described earlier to calculate average percentage signal change for each condition, used as the dependent variables in a second-level random-effects ANOVA.

For whole brain analyses, subject-specific signal change maps were calculated for contrasts of interest and resulting group statistical maps were overlaid on flattened inflated cortical projections in BrainVoyager.

RESULTS

We used two complementary measures of position selectivity. First, we measured differences in the magnitude of activity evoked by stimuli falling in the contralateral versus ipsilateral visual field. Second, we compared the effect of repeating stimuli in the same visual hemifield to the effect of repeating stimuli in opposite hemifields. ANOVA revealed no effect of hemisphere on either of these effects; therefore we combined data from right and left hemisphere structures for each subject before performing the subsequently detailed analyses. In the adaptation analysis, for each hemisphere we first considered

only responses in blocks in which the contralateral visual field was the “adapted” visual field. For example, for right hemisphere structures, data were drawn only from Fixed blocks in which stimuli appeared in the left hemifield, and from Cross blocks in which the *second* stimulus appeared in the left hemifield. We present a subset of results from the complementary hemifield (i.e., ipsilateral hemifield) in a later section.

Contralateral bias

As a preliminary analysis of position selectivity, we compared activity evoked during blocks with stimuli limited to either the contralateral or the ipsilateral visual field (Fig. 2, *top*). For this analysis, data were combined from Fixed-Novel and Fixed-Repeat blocks. With scene stimuli, responses to stimuli in the contralateral visual field were significantly higher than responses in the ipsilateral visual field in all scene-selective ROIs [two-tailed paired *t*-test; PPA, $t(9) = 5.0$, $P = 4 \times 10^{-4}$; RSC, $t(9) = 3.04$, $P = 0.014$; TOS, $t(8) = 5.43$, $P = 2 \times 10^{-4}$], as well as in LOC [$t(9) = 6.94$, $P = 3 \times 10^{-5}$]. The relative magnitudes of contralateral bias varied among these regions, although in all cases responses to ipsilateral scenes reached $\geq 50\%$ of the strength of responses to contralateral scenes. Responses to objects (Fig. 2, *bottom*) showed significant contralateral bias in the PPA, TOS, and LOC, but not RSC [PPA, $t(8) = 3.29$, $P = 0.0055$; TOS, $t(7) = 3.88$, $P = 0.0023$; LOC, $t(8) = 7.47$, $P = 4 \times 10^{-5}$; RSC, $t(8) = 1.03$, $P = 0.22$].

Scene adaptation

Although all ROIs had significantly higher responses to contralateral than to ipsilateral stimuli during Fixed blocks, responses to ipsilateral stimuli were sizeable. Ipsilateral responses could be explained either by neurons with large RFs centered in the contralateral field but extending across the vertical meridian or by neurons with small RFs that tiled both visual fields. As these observations indicate, raw hemodynamic response magnitudes are informative of the range of stimulus

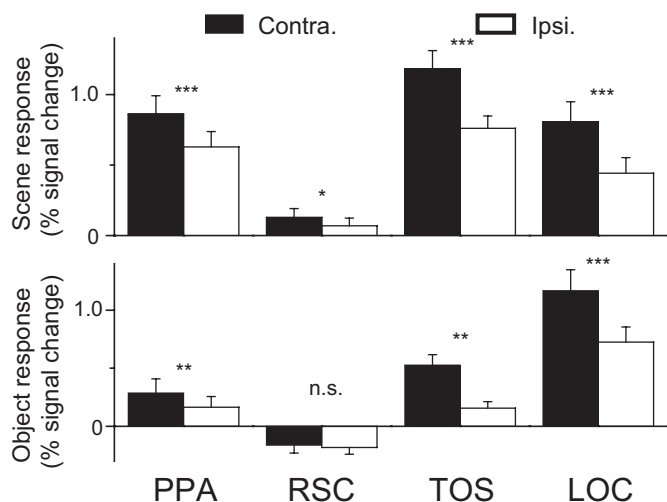


FIG. 2. Contralateral preference in functional magnetic resonance imaging (fMRI) response. Hemodynamic signals for stimuli restricted to either the contralateral or ipsilateral visual field were averaged across hemispheres for all subjects for scenes (*top*, $n = 10$) and objects (*bottom*, $n = 9$). Signals were average of Fixed-Novel and Fixed-Repeat blocks in each hemifield. Error bars are 1 SE. n.s., not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

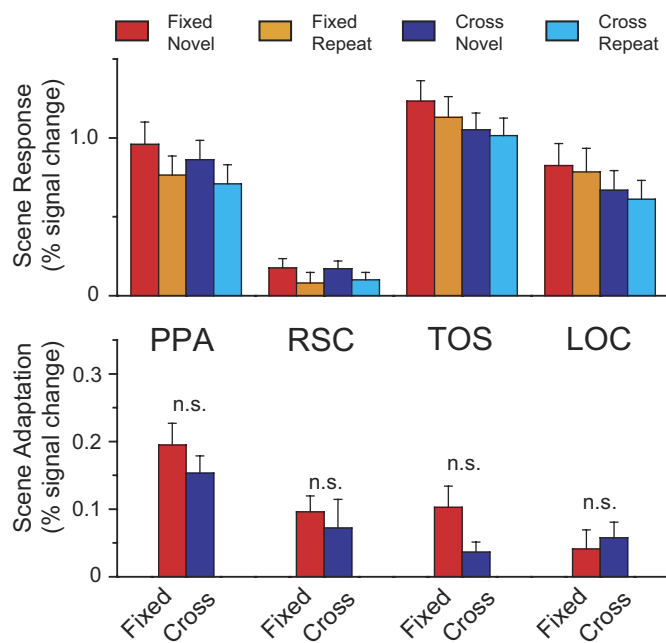


FIG. 3. fMRI adaptation effects for scenes. *Top*: response in all 4 conditions. *Bottom*: comparison of the magnitude of the same-hemifield adaptation effect (Fixed-Novel minus Fixed-Repeat) to the magnitude of the cross-hemifield adaptation effect (Cross-Novel minus Cross-Repeat). Adaptation magnitudes did not differ significantly between Fixed and Cross blocks in any of the 4 regions of interest (ROIs), suggesting an absence of position specificity. Error bars are 1 SE.

positions that a neuronal population responds to, but reveal little about the RF sizes of individual neurons.

To address this issue, we used an adaptation-based approach previously developed by McKyton and Zohary (2007) to examine topography in LOC (see METHODS). Of particular interest was the extent to which adaptation effects (differences between Novel and Repeat blocks) varied depending on whether repeated stimuli appeared in the same visual hemifield or in opposite hemifields (Fixed vs. Cross). If RFs extended across the vertical meridian, we expected that adaptation effects would be roughly as large for Cross blocks as for Fixed blocks because stimuli appearing in opposite hemifields would activate the same neurons. On the other hand, if RFs did not extend across the vertical meridian, then stimuli appearing in opposite hemifields would activate different neural sets, and adaptation during Cross blocks should be reduced compared with adaptation during Fixed blocks.

Adaptation effects are illustrated in Fig. 3. ANOVA revealed a significant main effect of scene repetition (Novel > Repeat) in all ROIs [PPA, $F(1,9) = 151.23$, $P < 10^{-5}$; RSC, $F(1,9) = 18.64$, $P = 0.002$; TOS, $F(1,8) = 17.93$, $P = 0.003$; LOC $F(1,9) = 7.45$, $P = 0.023$] and a significant main effect of Fixed versus Cross in the PPA [$F(1,9) = 7.13$, $P = 0.026$], TOS [$F(1,8) = 14.65$, $P = 0.005$], and LOC [$F(1,9) = 28.93$, $P = 4 \times 10^{-4}$], but not RSC [$F(1,9) = 0.067$, $P = 0.8$]. The Fixed versus Cross differences are attributable to the fact that more stimuli were presented in the contralateral visual field during Fixed blocks than during Cross blocks and thus reflect the contralateral response bias in these regions.

Critically, there was no evidence for any interaction between the Fixed/Cross and Novel/Repeat factors in the PPA [$F(1,9) = 0.67$, $P = 0.43$], RSC [$F(1,9) = 0.181$, $P = 0.68$],

or LOC [$F(1,9) = 0.2, P = 0.67$]. Although there was a trend toward an interaction in TOS, it fell short of significance [$F(1,8) = 3.19, P = 0.11$]. In other words, the strength of adaptation in these regions did not vary significantly, depending on whether stimuli were repeated in the same or opposite hemifields (Fig. 3, *bottom*). This result suggests that scenes in different hemifields activated either the same or highly overlapping populations of neurons, and thus argues that individual neurons were sensitive to scenes falling on both sides of the vertical meridian.

Object adaptation

The absence of any significant differences between scene adaptation effects in Fixed and Cross blocks suggests that neurons in the PPA and RSC possessed RFs large enough to encompass the stimulus positions in both hemifields. We sought to validate our technique by replicating previous work demonstrating position-selective adaptation in LOC for objects. McKyton and Zohary (2007), using the same adaptation comparisons we used, found significantly greater object adaptation in Fixed than in Cross blocks in LOC, and concluded from this that receptive fields in this region were confined to a single visual field. We attempted to replicate these results by repeating the adaptation experiment using objects in lieu of scenes in nine of our ten subjects. This manipulation turned out to be critical given our observation of position invariance rather than position specificity in LOC with scenes.

All aspects of the experiment were the same as for scenes, with the exception of the task: similar to McKyton and Zohary, subjects were asked to silently name each object as it appeared on the screen, while maintaining central fixation. As with scenes, repeated objects produced significant adaptation in LOC [$F(1,8) = 26.59, P = 6 \times 10^{-4}$], the PPA [$F(1,8) = 12.86, P = 0.007$], and TOS [$F(1,7) = 30.0, P = 9 \times 10^{-4}$] (Fig. 4). There was no significant main effect of object repetition in RSC [$F(1,8) = 0.021, P = 0.89$]. A significant main effect of Fixed versus Cross was observed in LOC [$F(1,8) = 17.48, P = 0.003$] and, to a lesser extent, in TOS [$F(1,7) = 5.76, P = 0.047$], but not the PPA [$F(1,8) = 1.39, P = 0.27$] nor RSC [$F(1,8) = 0.19, P = 0.68$].

Critically, object adaptation effects in Cross blocks were significantly smaller than those in Fixed blocks in LOC (Fig. 4, *bottom*), as demonstrated by a highly significant interaction between Fixed/Cross and Novel/Repeat [$F(1,8) = 30.64, P = 6 \times 10^{-4}$]. This interaction was also significant in TOS [$F(1,7) = 7.0, P = 0.034$], but not in the PPA [$F(1,8) = 0.37, P = 0.56$] nor RSC [$F(1,8) = 0.095, P = 0.77$]. In sum, adaptation effects for objects were position specific in LOC and TOS, but position invariant in the PPA and RSC.

The position specificity for objects in LOC replicates previous results indicating that RFs in this region are largely confined to one hemifield, and contrasts notably with the position invariance for scenes (and objects) in the PPA. We directly assessed differences in adaptation patterns between the PPA and LOC by performing a $2 \times 2 \times 2$ ANOVA including ROI as a factor. Because neither scenes nor objects elicited strong responses in both the PPA and LOC, we used data from those stimuli that best activated each region: scenes for the PPA and objects for LOC. We found a significant three-way interaction between the ROI, Fixed/Cross, and Novel/Repeat

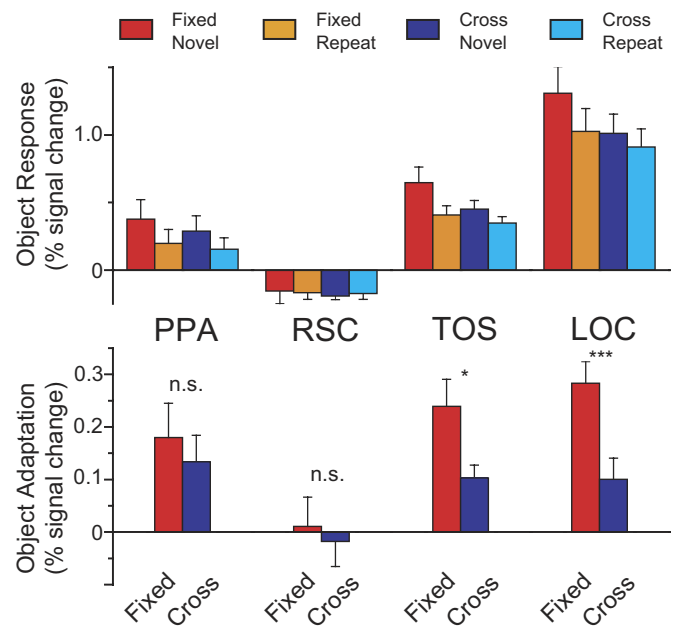


FIG. 4. fMRI adaptation effects for objects. *Top*: response in all 4 conditions. *Bottom*: comparison of the magnitude of same- and cross-hemifield adaptation effects. Adaptation in Fixed blocks was significantly greater than in Cross blocks in both lateral occipital complex (LOC) and transverse occipital sulcus (TOS), indicating position specificity. Error bars are 1 SE.

factors [$F(1,8) = 6.26, P = 0.037$], indicating that the Fixed/Cross adaptation difference was significantly greater for objects in LOC than for scenes in the PPA.

As is standard in the literature, we defined LOC as those voxels that exhibited significantly higher responses to objects than to scrambled objects. This definition may group together several contiguous subregions that are functionally heterogeneous and may possess different degrees of retinotopic organization (Larsson and Heeger 2006; Sawamura et al. 2005). To assess whether position specificity extended across all of LOC, we divided each subject's LOC into anterior and posterior segments, a task made easy by the tendency for object-selective activity to localize at two foci along the rostrocaudal axis (Fig. 5A). We further refined these two regions by excluding any voxels that were also included in the PPA. Additionally, because of the close proximity of each of these regions to each other and to the PPA, for this analysis we did not spatially smooth the fMRI data.

Both posterior LOC (pLOC) and anterior LOC (aLOC) responded more strongly to stimuli in the contralateral visual field than to stimuli in the ipsilateral visual field [Fig. 5B: aLOC, $t(8) = 5.38, P = 6 \times 10^{-4}$; pLOC, $t(8) = 5.56, P = 6 \times 10^{-4}$]. Furthermore, both pLOC and aLOC showed significantly greater adaptation in Fixed blocks than in Cross blocks (Fig. 5C), as demonstrated by significant interactions between Fixed/Cross and Novel/Repeat factors in both subregions [pLOC, $F(1,8) = 8.67, P = 0.019$; aLOC, $F(1,8) = 7.59, P = 0.025$]. Although there was a trend for the Fixed versus Cross adaptation difference to be larger in pLOC than aLOC, consistent with a gradient in RF sizes along the rostrocaudal axis, a $2 \times 2 \times 2$ ANOVA with ROI as a factor found this trend to be nonsignificant [$F(1,8) = 1.19, P = 0.31$]. In sum, the adaptation patterns in both pLOC and aLOC were consis-

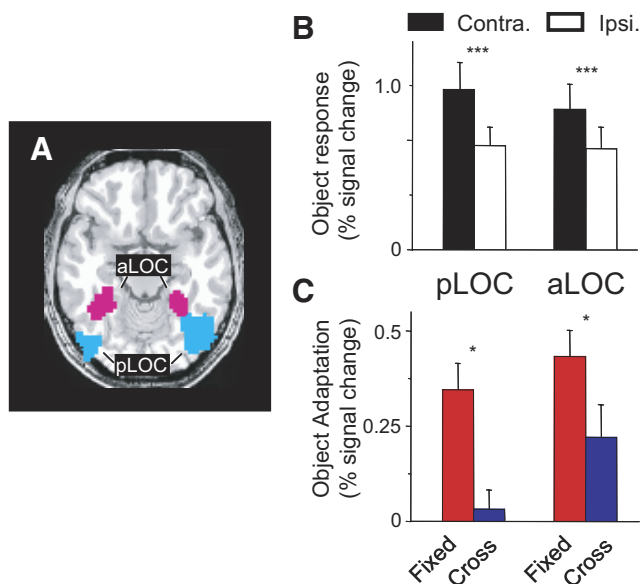


FIG. 5. Responses to objects in LOC subregions. *A*: after identification based on functional localizer scans, LOC in each subject was divided into anterior (aLOC) and posterior (pLOC) subregions, shown here for one subject. *B*: averaged across subjects, pLOC and aLOC both showed significantly higher responses to objects in the contralateral hemifield than in the ipsilateral hemifield. *C*: consistent with the overall LOC pattern, both aLOC and pLOC showed significantly greater adaptation in Fixed blocks than in Cross blocks. Error bars are 1 SE.

tent with the overall adaptation pattern for LOC shown in Fig. 4.

Object adaptation in the ipsilateral hemifield

At first glance, the conclusion that RFs for object-responsive neurons in LOC are largely confined to one hemifield may appear inconsistent with sizeable LOC response to ipsilateral object presentations. However, once again, it is important to remember that adaptation effects are more informative about the RF sizes of individual neurons, whereas the overall response is more informative about the range of RF locations across the population. Although the greater amount of adaptation in LOC during Fixed blocks than during Cross blocks suggests that identical objects appearing in different hemifields activate substantially different populations of neurons, these populations need not be segregated into different hemispheres. Indeed, the large response to ipsilateral stimulation suggests that LOC may contain neurons whose RFs are centered in the ipsilateral hemifield.

To test this, we examined object adaptation effects when stimuli appeared in the ipsilateral hemifield during Fixed blocks. (Note that up to this point, we have considered only adaptation effects for the contralateral hemifield.) Ipsilateral adaptation effects during Fixed blocks were significant in LOC [$F(1,8) = 55.8$, $P = 7 \times 10^{-5}$], the PPA [$F(1,8) = 10.8$, $P = 0.011$], and TOS [$F(1,7) = 15.1$, $P = 0.006$], but not in RSC [$F(1,8) = 1.71$, $P = 0.28$]. Indeed, there was no significant difference in the magnitude of ipsilateral and contralateral adaptation effects [LOC, $F(1,8) = 0.051$, $P = 0.83$; PPA, $F(1,8) = 2.6$, $P = 0.15$; TOS, $F(1,7) = 1.27$, $P = 0.30$]. For the PPA these results can be interpreted by assuming that stimuli appearing in the ipsilateral visual field activate the same

neurons as stimuli appearing in the contralateral visual field. However, for TOS and LOC, the prior evidence for smaller RFs makes this explanation infeasible. Rather, the results suggest that these regions contain neurons with RFs centered in both hemifields.

The fact that adaptation effects were equivalent for ipsilateral and contralateral stimuli in LOC and TOS (Fig. 6) suggests that both stimuli activated a similar number of neurons. However, this conclusion is inconsistent with the observation of higher overall activity for contralateral stimuli than for ipsilateral stimuli in these regions. This apparent contradiction indicates that adaptation effects may not be strictly linear with respect to activation, a point we explore further in the DISCUSSION.

Whole brain analysis

Our principal goal in this study was to understand the level of position specificity among scene-selective ROIs. However, we were also interested in patterns of adaptation evoked by our stimuli in other areas of the brain. Given that scenes produced roughly equivalent adaptation in Fixed and Cross blocks for each of the ROIs we analyzed, we were particularly interested in identifying regions for which there was a significant effect of stimulus location on scene adaptation.

Figure 7*A* presents a flattened cortex map of *P* values for the Fixed/Cross by Novel/Repeat interaction for scenes, drawn from those voxels that showed significant Fixed adaptation (paired *t*-test, $P < 0.01$). Overlaid on the maps are boundaries of each ROI analyzed earlier, defined from average localizer data across all 10 subjects. Consistent with ROI analyses, regions within all ROIs are predominantly blue, indicating no significant differences between adaptation in Fixed and Cross blocks.

By and large, areas with significantly larger Fixed than Cross adaptation effects fell outside our ROIs. The strongest interactions were found in a right hemisphere region adjacent to functionally defined TOS corresponding to the cuneus/precuneus, structures that are frequently activated during saccade preparation and redirection of covert attention (Berman et al. 1999; Petit and Beauchamp 2003; Woldorff et al. 1997). Because subjects were forced to shift attention frequently in

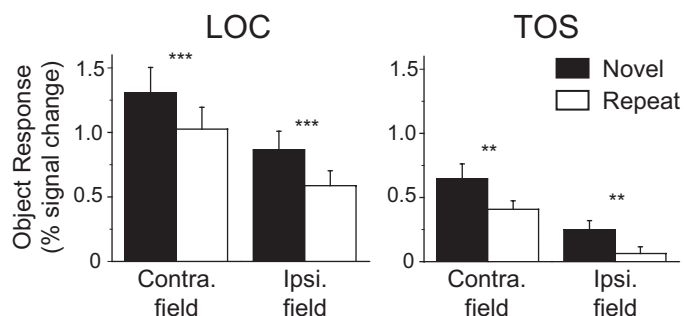


FIG. 6. Object adaptation effects for stimuli presented in the contra- and ipsilateral hemifields in LOC and TOS. For each region and hemisphere, adaptation effects for Fixed blocks in which all stimuli were presented into contralateral hemifield (e.g., left visual field for right LOC) are compared with adaptation effects when all stimuli are presented in the ipsilateral hemifield. Adaptation effects did not depend on hemifield, suggesting equivalent representations of each hemifield for the stimulus locations we used. Error bars are 1 SE.

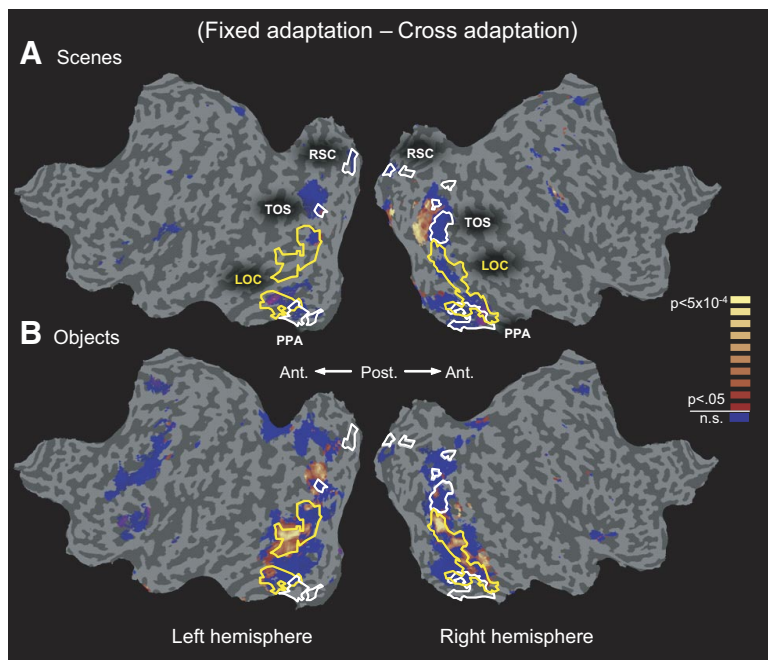


FIG. 7. Group analysis of adaptation differences between Fixed and Cross blocks for scenes (A) and for objects (B). A: consistent with ROI analyses, functional ROIs coincided with regions showing no significant difference between Fixed and Cross adaptation effects for scenes (blue). Regions showing significantly greater Fixed adaptation (red/yellow) were found outside our ROIs, notably in the cuneus and precentral gyrus. B: significantly greater Fixed adaptation for objects was localized mainly within the LOC and immediately adjacent regions. For both scenes and objects, maps are limited to those voxels that showed significant adaptation effects in Fixed blocks. Flattened maps were generated from results of random-effects analysis across all subjects ($n = 10$ for scenes, $n = 9$ for objects). Contrast of interest was [(Fixed-*Novel* minus Fixed-*Repeat*) - (Cross-*Novel* minus Cross-*Repeat*)]; only voxels showing significant fixed adaptation are colored. ROIs were defined from a random-effects group analysis of functional localizer data at a threshold of $P < 0.01$, uncorrected.

Cross blocks, increased activity among networks mediating attention may have partially masked adaptation effects that might otherwise have been apparent. This interaction was absent from the left hemisphere.

Figure 7B shows interaction data for object stimuli. Consistent with ROI analysis, voxels with significantly greater Fixed adaptation are centered on LOC and extend into TOS, both of which showed significantly greater Fixed adaptation in ROI analysis. Similar to scenes, we also found significantly greater Fixed adaptation than Cross adaptation in an area outside our ROIs near the intraparietal sulcus, although (opposite to the case with scenes) this region was apparent only in the left hemisphere.

DISCUSSION

In this study, we used fMRI adaptation to characterize the position specificity of neurons in scene-selective regions PPA, RSC, and TOS, as well as in object-selective LOC. We found that the strengths of adaptation effects in the PPA and RSC did not depend on whether stimuli are repeated in the same or opposite hemifields. This suggests that scene processing in these regions is largely insensitive to retinal position for the range of stimulus positions we used. In contrast, adaptation effects for objects in LOC were significantly stronger when objects were repeated in the same hemifield than when they were repeated in opposite hemifields, suggesting position specificity. This latter result is consistent with previous work (Larsson and Heeger 2006; McKyton and Zohary 2007; Niemeier et al. 2005; Yoshor et al. 2006), thereby providing validation of our adaptation technique. Taken as a whole, our results suggest a distinction between neurons in object- and scene-selective regions in the level of information about stimulus position each population encodes. RFs in scene-selective regions appear to be larger than in LOC, consistent with the hypothesis that they signal the presence of large-scale features unique to ambient scenes.

Scene-selective regions

A central role for the PPA in scene perception and spatial navigation has been appreciated for some time (Aguirre et al. 1996, 1998; Barrash et al. 2000; Bohbot et al. 1998; Burgess et al. 2001; Epstein and Kanwisher 1998; Epstein et al. 2001; Goh et al. 2004; Janzen and van Turenout 2004; Kohler et al. 2002; Maguire et al. 1998). The PPA is activated under a wide range of situations in which scenes are viewed or imagined, including passive viewing of scenes (Epstein and Kanwisher 1998), performance of a one-back matching task on scenes (Epstein et al. 1999), navigation through virtual reality environments (Maguire et al. 1998), and recovery of topographical information (Burgess et al. 2001; O'Craven and Kanwisher 2000; Rosenbaum et al. 2004). Furthermore, the PPA responds strongly to a wide variety of scenes, including both photographs of real-world locations and images of table-top Lego models (Epstein et al. 1999, 2003). The range of tasks and stimuli for which the PPA is active has made it difficult to determine the specific aspects of these stimuli that drive its neurons. Are they driven by local features, such as objects, shapes, and contour intersections, that are frequently found in scenes? Or are they driven by global features that are unique to scenes, such as large extended surfaces, or the particular relationships among objects and features that help define a three-dimensional space? The relatively high degree of spatial invariance for adaptation we found in the PPA with scenes suggests that scene-selective neurons in the PPA possess large RFs. This result is consistent with the idea that the PPA encodes information about large-scale arrangements of surfaces, features, and objects within scenes.

In spite of this, the PPA responded to more local features as well, demonstrated by the significant activation and adaptation effects produced by objects. This finding is consistent with earlier results indicating that the PPA responds substantially more strongly to nonscene objects than to faces or a blank screen (Epstein and Kanwisher 1998), especially when the

objects have the potential to act as orienting landmarks (Janzen and van Turenout 2004). The current data do not allow us to determine whether these responses reflected weak activation of scene-selective neurons, or activation of a distinct class of object-selective cells. Regardless, adaptation effects for objects were the same for Fixed and Cross blocks, suggesting that object-responsive neurons expressed the same high level of position invariance as scene-responsive neurons. This pattern contrasts notably with the LOC response to objects, which was much more position specific. We hypothesize that this difference may reflect different goals for the PPA and LOC in object perception. In particular, LOC may process objects for purposes of object identification, whereas the PPA may respond to objects only to the extent that they aid identification of the places within which they are embedded.

Somewhat surprisingly, the magnitude of the adaptation effect for objects in the PPA was almost identical to the magnitude of the adaptation effect for scenes, even though scenes evoked much higher overall responses. The reasons for this are unclear, but this finding is consistent with results of previous fMRI studies showing equivalent adaptation effects for preferred and nonpreferred stimuli (Avidan et al. 2002), as well as with similar physiological results in macaques (Sawamura et al. 2006; their Fig. 2).

As in the PPA, adaptation in RSC was invariant to retinal position. Previous studies have shown that the RSC response to scenes is higher when the scenes act as a cue for topographical memory-retrieval tasks than during simple scene viewing, and that RSC responds more strongly to scenes depicting familiar location than to scenes depicting unfamiliar locations (Epstein et al. 2007; Sugiura et al. 2005). Based on these results, we have proposed that RSC is less involved than the PPA in scene perception per se, but more involved in using information about the local scene to orient the observer relative to spatial frameworks that extend beyond what is currently visible. Because the position of a scene or its elements in retinotopic or even egocentric coordinates has little consequence for its relationship to other, unseen, locations, this hypothesis is consistent with our finding that neurons in RSC are insensitive to the position of a scene in visual space. It is also interesting that the overall response to scenes in RSC was relatively small compared with the response observed in earlier experiments (~25% of the PPA response, compared with ~50–75% in Epstein et al. 2007). This may be a consequence of the peripheral presentation: placing the scenes off-center may particularly influence the “place-ness” of the stimulus even though its perceptual features are retained. Thus the small response in RSC is consistent with the hypothesis that this region plays more of a role in spatial memory than in scene perception.

Less is known about scene selectivity in TOS, which, like the PPA and RSC, did not show significantly greater adaptation in Fixed blocks than in Cross blocks, although this difference was greater in TOS than in either of the other scene-selective ROIs. Like the PPA, TOS is known to show a preference for stimuli falling in the visual periphery (Levy et al. 2004). Our results suggest that neurons in TOS tend to possess smaller RFs than those in neurons in the PPA or RSC, and thus may constitute an earlier step in the scene-processing hierarchy.

Object-selective regions

Although the emphasis of this study was on scene-selective rather than object-selective regions, we included LOC in our analysis as a way to validate the results of our adaptation analysis. Consistent with previous reports, our results suggest that objects falling in opposite hemifields activated substantially different populations of neurons in LOC (McKyton and Zohary 2007; Niemeier et al. 2005). Taken together with the pattern of adaptation evoked by scenes in the PPA, our results suggest that the average RF was smaller in LOC than in the PPA.

It should be noted that this conclusion is based on the assumption that the adaptation we observed reflects attenuation of the spiking responses of neurons located within LOC, a premise that may not be valid under all circumstances (Grill-Spector et al. 2006; Krekelberg et al. 2006; Sawamura et al. 2006). For example, in a single-unit study of macaque IT, Sawamura et al. (2006) showed that repetition-based adaptation effects were more narrowly tuned for stimulus identity than neurons' spiking responses, insofar as the adaptation effects were sensitive to differences between stimuli to which the neuron responded equally. One possible explanation for this is that a portion of adaptation effects may, under some conditions, reflect attenuation of the synaptic inputs to the neuron rather than attenuation of the neuron itself, and thus might more strongly reflect the response properties of the neurons providing the inputs (Kohn and Movshon 2003; Krekelberg et al. 2006). In our experiment, it is thus possible that the position-specific adaptation we observed in LOC reflects the RF sizes of neurons providing input to LOC, and that LOC neurons actually possess RFs larger than our results would lead us to believe. It should be noted, however, that while Sawamura et al. (2006) found that adaptation tuning tended to be narrower than that of spiking responses, they also noted that the difference between adaptation tuning and neural tuning was most pronounced for early repetitions, but less noticeable after many repetitions. This suggests that block designs such as ours may be less vulnerable to inherited adaptation than event-related designs.

In addition to showing adaptation effects for repeated objects, LOC also showed small but significant adaptation effects for repeated scenes. Surprisingly, the position specificity of LOC adaptation for scenes differed from that observed with objects. With objects, LOC showed much greater adaptation in Fixed blocks than in Cross blocks, whereas with scenes LOC showed no significant difference between Fixed and Cross adaptation. The reason for this difference is unclear. We consider it unlikely that it arose from the different attentional demands of the two tasks. Although the scene task (blur detection) likely required greater attention than the object task (silent naming), previous work has shown that attention causes constriction of RFs (Connor et al. 1997; Moran and Desimone 1985). Thus any effect of attention would have worked *against* the pattern we saw. It is possible that the meager levels of adaptation evoked by scenes simply do not allow differences between Fixed and Cross adaptation to be distinguished.

Another interesting aspect of the data was the fact that Fixed adaptation effects in LOC were equivalently strong for stimuli in the contra- and ipsilateral hemifields. This would seem to indicate that equally sized populations responded to stimuli in

the two hemifields, a conclusion at odds with a simple comparison of raw responses to contra- and ipsilateral stimulation. This conflict is similar to our observation that adaptation effects in the PPA were about the same for both scenes and objects; in both cases, less-effective stimuli showed the same absolute level of adaptation as more-effective stimuli. We are not the first to report this phenomenon. In the original LOC experiments that our study replicates, McKyton and Zohary (2007) reported similar adaptation levels for ipsi- and contralateral stimuli, despite a large response difference (their Fig. 3C; note similar LH and RH alter4 and alter2 differences). Similarly, Avidan et al. (2002) found that adaptation in both LOC and fusiform gyrus produced by repeated houses was not significantly different from repeated faces, even though faces evoked higher “unadapted” responses. Taken together with our data, these results suggest some nonlinearity in the strength of adaptation with respect to overall activity in LOC and call for caution in the interpretation of adaptation results. In our study, though, any such nonlinearity does not influence our principal finding that adaptation effects were greater for Fixed than for Cross blocks, nor the conclusion that LOC RFs are largely confined to one hemifield. If anything, any error introduced by adaptation nonlinearities led us to overestimate LOC RF dimensions.

Implications for the role of the PPA in scene processing

Earlier reports from our laboratory indicate that fMRI adaptation effects in the PPA are largely viewpoint specific, especially when the effects of immediate stimulus repetition are considered (Epstein et al. 2003, 2005). In other words, when photographs of the same scene taken from the same view are presented in succession, substantial adaptation is observed, but adaptation is smaller (or even nonexistent) when successive photographs depict the same scene from different viewpoints. At first glance, these results may appear to be in conflict with the position invariance we found: if neurons in the PPA are insensitive to large changes in the retinal position of a scene, why should they show specificity for different views of the same scene? The most straightforward account of these results is that neurons in these regions, given their large RFs, principally convey information about the spatial relationships among scene elements (including the spatial relationships between those elements and the body), rather than the absolute locations of these elements in visual space. When viewpoint changes, these relationships necessarily change as well, leading to adaptation effects that are viewpoint specific. On the other hand, when a scene—viewed from a fixed point, as in our experiment—simply translates on the retina, these relationships remain unchanged and position-invariant adaptation is observed.

The utility of neurons possessing viewpoint specificity but position invariance is clear. Sensitivity to viewpoint is useful if the task is to signal changes in the observer’s location and orientation with respect to the local physical environment. On the other hand, position invariance ensures a static representation of the visual environment across eye movements, which convey no information about changes in the observer’s location and orientation. In sum, the observed pattern is what we might expect from a cortical region that is sensitive to visual changes caused by bodily movements made during navigation.

How far does position invariance in the PPA go? We can only say that scene-selective neurons in the PPA appear to have, on average, RFs large enough to cover stimuli falling in opposite hemifields within 11° of the vertical meridian. How much further this invariance may extend is unclear. A completely invariant representation of the visual environment may not be physiologically plausible. However, a high level of position invariance in the PPA relative to other visual areas may be sufficient to support scene recognition and navigation under most circumstances. Further, our results suggest that RFs in the PPA tend to be larger than those in object-selective cortex, which physiological recordings in macaque have shown possess among the greatest dimensions recorded. This strongly supports the hypothesis that scene preference in the PPA is derived from the capacity of neurons in those regions to integrate information over large regions of visual space, thus allowing them to encode large-scale features specific to ambient scenes.

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REFERENCES

- Aggelopoulos NC, Rolls ET.** Scene perception: inferior temporal cortex neurons encode the positions of different objects in the scene. *Eur J Neurosci* 22: 2903–2916, 2005.
- Aguirre GK, D’Esposito M.** Topographical disorientation: a synthesis and taxonomy. *Brain* 122: 1613–1628, 1999.
- Aguirre GK, Detre JA, Alsop DC, D’Esposito M.** The parahippocampus subserves topographical learning in man. *Cereb Cortex* 6: 823–829, 1996.
- Aguirre GK, Zarahn E, D’Esposito M.** An area within human ventral cortex sensitive to “building” stimuli: evidence and implications. *Neuron* 21: 373–383, 1998.
- Avidan G, Hasson U, Hendler T, Zohary E, Malach R.** Analysis of the neuronal selectivity underlying low fMRI signals. *Curr Biol* 12: 964–972, 2002.
- Barrash J, Damasio H, Adolphs R, Tranel D.** The neuroanatomical correlates of route learning impairment. *Neuropsychologia* 38: 820–836, 2000.
- Berman RA, Colby CL, Genovese CR, Voyvodic JT, Luna B, Thulborn KR, Sweeney JA.** Cortical networks subserving pursuit and saccadic eye movements in humans: an FMRI study. *Hum Brain Mapp* 8: 209–225, 1999.
- Bohbot VD, Kalina M, Stepankova K, Spackova N, Petrides M, Nadel L.** Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia* 36: 1217–1238, 1998.
- Boussaoud D, Desimone R, Ungerleider LG.** Visual topography of area TEO in the macaque. *J Comp Neurol* 306: 554–575, 1991.
- Burgess N, Maguire EA, Spiers HJ, O’Keefe J.** A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. *Neuroimage* 14: 439–453, 2001.
- Connor CE, Preddie DC, Gallant JL, Van Essen DC.** Spatial attention effects in macaque area V4. *J Neurosci* 17: 3201–3214, 1997.
- DiCarlo JJ, Maunsell JH.** Anterior inferotemporal neurons of monkeys engaged in object recognition can be highly sensitive to object retinal position. *J Neurophysiol* 89: 3264–3278, 2003.
- Epstein RA.** The cortical basis of visual scene processing. *Vis Cogn* 12: 954–978, 2005.
- Epstein RA, DeYoe EA, Press DZ, Rosen AC, Kanwisher N.** Neuropsychological evidence for a topographical learning mechanism in parahippocampal cortex. *Cogn Neuropsych* 18: 481–508, 2001.
- Epstein RA, Graham KS, Downing PE.** Viewpoint-specific scene representations in human parahippocampal cortex. *Neuron* 37: 865–876, 2003.
- Epstein RA, Harris A, Stanley D, Kanwisher N.** The parahippocampal place area: Recognition, navigation, or encoding? *Neuron* 23: 115–125, 1999.

- Epstein RA, Higgins JS.** Differential parahippocampal and retrosplenial involvement in three types of visual scene recognition. *Cereb Cortex* 17: 1680–1693, 2007.
- Epstein RA, Higgins JS, Jablonksi K, Feiler A.** Visual scene processing in familiar and unfamiliar environments. *J Neurophysiol* 97: 3670–3683, 2007.
- Epstein RA, Higgins JS, Thompson-Schill SL.** Learning places from views: variation in scene processing as a function of experience and navigational ability. *J Cogn Neurosci* 17: 73–83, 2005.
- Epstein RA, Kanwisher N.** A cortical representation of the local visual environment. *Nature* 392: 598–601, 1998.
- Goh JOS, Siong SC, Park D, Gutchess A, Hebrank A, Chee MWL.** Cortical areas involved in object, background, and object-background processing revealed with functional magnetic resonance adaptation. *J Neurosci* 24: 10223–10228, 2004.
- Grill-Spector K.** The neural basis of object perception. *Curr Opin Neurobiol* 13: 159–166, 2003.
- Grill-Spector K, Malach R.** fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychologica* 107: 293–321, 2001.
- Gross CG, Rocha-Miranda CE, Bender DB.** Visual properties of neurons in inferotemporal cortex of the macaque. *J Neurophysiol* 35: 96–111, 1972.
- Hartline HK.** The response of single optic nerve fibers of the vertebrate eye to illumination of the retina. *Am J Physiol* 121: 400–415, 1938.
- Hasson U, Harel M, Levy I, Malach R.** Large-scale mirror-symmetry organization of human occipito-temporal object areas. *Neuron* 37: 1027–1041, 2003.
- Henderson JM, Hollingworth A.** High-level scene perception. *Annu Rev Psychol* 50: 243–271, 1999.
- Intraub H.** The representation of visual scenes. *Trends Cogn Sci* 1: 217–222, 1997.
- Ishai A, Ungerleider LG, Martin A, Schouten HL, Haxby JV.** Distributed representation of objects in the human ventral visual pathway. *Proc Natl Acad Sci USA* 96: 9379–9384, 1999.
- Janzen G, van Turenout M.** Selective neural representation of objects relevant for navigation. *Nat Neurosci* 7: 673–677, 2004.
- Kohler S, Crane J, Milner B.** Differential contributions of the parahippocampal place area and the anterior hippocampus to human memory for scenes. *Hippocampus* 12: 718–723, 2002.
- Kourtzi Z, Kanwisher N.** Representation of perceived object shape by the human lateral occipital complex. *Science* 293: 1506–1509, 2001.
- Larsson J, Heeger DJ.** Two retinotopic visual areas in human lateral occipital cortex. *J Neurosci* 26: 13128–13142, 2006.
- Levy I, Hasson U, Avidan G, Hendler T, Malach R.** Center-periphery organization of human object areas. *Nat Neurosci* 4: 533–539, 2001.
- Levy I, Hasson U, Harel M, Malach R.** Functional analysis of the periphery effect in human building related areas. *Hum Brain Mapp* 22: 15–26, 2004.
- Logothetis NK, Sheinberg DL.** Visual object recognition. *Annu Rev Neurosci* 19: 577–621, 1996.
- Maguire EA.** The retrosplenial contribution to human navigation: a review of lesion and neuroimaging findings. *Scand J Psychol* 42: 225–238, 2001.
- Maguire EA, Burgess N, Donnett JG, Frackowiak RS, Frith CD, O'Keefe J.** Knowing where and getting there: a human navigation network. *Science* 280: 921–924, 1998.
- McKyton A, Zohary E.** Beyond retinotopic mapping: the spatial representation of objects in the human lateral occipital complex. *Cereb Cortex* 17: 1164–1172, 2007.
- Mendez MF, Cherrier MM.** Agnosia for scenes in topographagnosia. *Neuropsychologia* 41: 1387–1395, 2003.
- Moran J, Desimone R.** Selective attention gates visual processing in the extrastriate cortex. *Science* 229: 782–784, 1985.
- Nakamura K, Kawashima R, Sato N, Nakamura A, Sugiura M, Kato T, Hatano K, Ito K, Fukuda H, Schormann T, Zilles K.** Functional delineation of the human occipito-temporal areas related to face and scene processing—a PET study. *Brain* 123: 1903–1912, 2000.
- Niemeier M, Goltz HC, Kuchinad A, Tweed DB, Vilis T.** A contralateral preference in the lateral occipital area: sensory and attentional mechanisms. *Cereb Cortex* 15: 325–331, 2005.
- O'Craven KM, Kanwisher N.** Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *J Cogn Neurosci* 12: 1013–1023, 2000.
- Olmos A, Kingdom FA.** A biologically inspired algorithm for the recovery of shading and reflectance images. *Perception* 33: 1463–1473, 2004.
- Petit L, Beauchamp MS.** Neural basis of visually guided head movements studied with fMRI. *J Neurophysiol* 89: 2516–2527, 2003.
- Rosenbaum RS, Ziegler M, Wincour G, Grady CL, Moscovitch M.** “I have often walked down this street before”: fMRI studies on the hippocampus and other structures during mental navigation of an old environment. *Hippocampus* 14: 826–835, 2004.
- Sawamura H, Orban GA, Vogels R.** Selectivity of neuronal adaptation does not match response selectivity: a single-cell study of the fMRI adaptation paradigm. *Neuron* 49: 307–318, 2006.
- Sugiura M, Shah NJ, Zilles K, Fink GR.** Cortical representations of personally familiar objects and places: functional organization of the human posterior cingulate cortex. *J Cogn Neurosci* 17: 183–198, 2005.
- Tanaka K.** Inferotemporal cortex and object vision. *Annu Rev Neurosci* 19: 109–139, 1996.
- Tovee MJ, Rolls ET, Treves A, Bellis RP.** Information encoding and the responses of single neurons in the primate temporal visual cortex. *J Neurophysiol* 70: 640–654, 1993.
- Woldorff MG, Fox PT, Matzke M, Lancaster JL, Veeraswamy S, Zamarripa F, Seabolt M, Glass T, Gao JH, Martin CC, Jerabek P.** Retinotopic organization of early visual spatial attention effects as revealed by PET and ERPs. *Hum Brain Mapp* 5: 280–286, 1997.
- Yoshor D, Bosking WH, Ghose GM, Mausell JRH.** Receptive fields in human visual cortex mapped with surface electrodes. *Cereb Cortex* (December 16, 2006). doi: 10.1093/cercor/bhl138. Online.