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Spatial vs. object specific attention in high-order visual areas

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Abstract

Recently we reported that the topographic organization of visual field eccentricity in human visual cortex extends into high-order, ventral occipitotemporal (VOT) cortex. Within this cortex, regions that respond preferentially to faces and buildings have specific eccentricity biases, suggesting that this category-eccentricity association may reflect differential needs of recognition processes. However, it is still not clear to what extent this center/periphery differentiation within high-order occipitotemporal cortex depends on immediate, moment-to-moment, task demands. Previous attention studies were confined either to exploring the visual field topography (spatial attention) or to object identity (object-based attention). Here, we combined the investigation of these two different attentional mechanisms in the same study. We found that the main source of attentional modulation in occipitotemporal cortex was object-based attention. Shifting attention to different object categories (buildings, faces, and arrows) substantially modulated the object-related activations. The differential activation to each object category in occipitotemporal object areas was maintained, albeit at a reduced level, even when attention was focused on different spatial locations. A slight eccentricity-related attentional differentiation was observed in the more dorsal lateral occipital region, but not in the VOT cortex. These results argue against the possibility that the source of the eccentricity differentiation in VOT cortex is due solely to moment-to-moment shifts in spatial attention mechanism and supports the notion that the eccentricity-biased maps found in this region are due to built-in shape selectivity established over long-term processes.

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Introduction

Our understanding of the organizing principles of the human occipitotemporal visual cortex has been growing rapidly in recent years. A number of functional mapping studies have revealed a complex network of specialized regions showing clear selectivity in their response properties for various object shapes. A particularly striking example is the mediolateral differentiation along ventral occipitotemporal cortex (VOT) in activation to face (Clark et al., 1996; Halgren et al., 1999; Kanwisher et al., 1997; Puce et al., 1995) and building images (Aguirre et al., 1998; Epstein and Kanwisher, 1998).

In parallel with this differentiation, we have recently

found evidence for a topographic organization in which, for identical object shapes, medial (building-related) occipitotemporal cortex, along the collateral sulcus, is activated preferentially to more peripheral stimuli compared to lateral (face-related) regions along the fusiform gyrus (Levy et al., 2001; Malach et al., 2002). Similar association with central field bias was found for letter strings and words (Hasson et al., 2002). This eccentricity-bias map is located in the VOT (Malach et al., 2002). We hypothesized that the category-eccentricity association may reflect differential needs of recognition processes for high cortical magnification (associated with central vision) or large-scale integration (associated with peripheral vision).

One aspect of this finding, which remains unresolved, is the extent to which the center/periphery differentiation depends on immediate, moment-to-moment task demands and the extent to which it is established through long-term

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developmental or learning effects. A prime instance of moment-to-moment modulation of task demands is the case of attentional shifts.

According to space-based theory of attention (Posner, 1980; Treisman and Gelade, 1980), attention can be directed to certain locations in space and hence can be metaphorically referred to as a “spotlight” having a variable size. Space-based attentional effects were indeed found in retinotopic visual areas (Brefczynski and DeYoe, 1999; Martinez et al., 1999; Somers et al., 1999; Tootell et al., 1998) but also in high-order object-related ones (Downing et al., 2001).

Following these findings, the center-periphery organization in the VOT might be explained as a by-product of varying spatial attentional demands. For example, whenever one encounters building images, which may require large-scale feature integration, a large spotlight of attention may be activated, leading to the peripherally biased collateral sulcus activation. While in encountering face images or letters, which require high acuity demands, a foveal spotlight of attention is recruited, leading to the centrally biased activation.

Alternatively, it could be that object identity, rather than spatial attention, is the dominant factor in determining the activation within those regions. Such a finding would be more compatible with an object-based attentional mechanism (Desimone and Duncan, 1995; Duncan, 1984; O’Craven et al., 1999; Vecera and Farah, 1994), according to which attention is directed toward specific objects rather than specific visual field locations.

Unfortunately, all studies of attentional modulations so far have focused separately either on spatial-attention or object-based attention. In the present work we tried to examine the nature of the attentional mechanisms found in high-order occipitotemporal cortex by combining the study of spatial attention and attention to object identity in the same experiment.

We found that when images of buildings and faces were contrasted while attention was shifted to different shapes, the level of shape-related activation was substantially modulated. In contrast, when spatial attention was modulated by attending to a central arrow or to a larger arrow in the periphery a slight eccentricity-related differentiation was observed in the lateral occipital region (LO) but not in the more ventral occipitotemporal cortex.

These results argue against shape-independent spatial attention as the major underlying source for the center-periphery differentiation of object areas in VOT. However, they are compatible with the notion that attentional effects in high-order object areas may depend on both spatial and object components.

Materials and methods

Subjects

Eight healthy subjects (4 women, ages 24–50 years) participated in the experiment. All subjects had normal or

corrected-to-normal vision and provided written informed consent. The Tel-Aviv Sourasky Medical Center approved the experimental protocol.

MRI setup

Subjects were scanned in a 1.5-T Signa Horizon LX 8.25 GE scanner equipped with a quadrature surface coil (Nova Medical Inc., Wakefield, MA) that covered the posterior brain regions. Blood oxygenation level-dependent (BOLD) contrast was obtained with gradient-echo echo-planar imaging (EPI) sequence (TR = 3000 ms, TE = 55 ms, flip angle = 90°, field of view 24 × 24 cm², matrix size 80 × 80). The scanned volume included 17 nearly axial slices of 4-mm thickness and 1-mm gap. T1-weighted high resolution (1 × 1 × 1 mm) anatomical images and three-dimensional (3D) spoiled gradient echo sequence were acquired on each subject to allow accurate cortical segmentation, reconstruction, and volume-based statistical analysis.

Visual stimulation

Stimuli were generated on a PC, projected via LCD projector (Epson MP 7200) onto a tangent screen positioned over the subject’s forehead, and viewed through a tilted mirror located above subjects’ eyes.

Experiments

Attention experiment

The experiment lasted 450 s, it included 10 different stimulus conditions, and had 57 epochs, which were presented in a counterbalanced block design paradigm, stimulus and blank epochs were interleaved. Each stimulus epoch lasted 9 s and each blank (fixation cross only) epoch lasted 6 s with the exception of the first and last blanks, which lasted 18 s each, blank epochs were repeated 29 times. A stimulus epoch consisted of 9 different stimuli; to minimize eye movements each stimulus was presented for 150 ms followed by 850 ms blank. Stimuli were 12 × 12-degree grayscale photos of faces and buildings. Superimposed on each image were three red dots that formed together a subjective arrowhead shape. The arrowhead was either small (0.96 × 1.64 degrees) located at the center of the image or large (6.2 × 12 degrees) and located in the periphery of the image (Fig. 1). The size of the dots composing the large arrowhead were enlarged to compensate for the magnification factor. The three dots composing the arrowhead were used instead of a full arrow, to ensure that judging the arrows’ direction could not be resolved by local information but would be based on global integration. This was especially crucial during the “large arrow” condition. Note that even if subjects may have adopted a strategy of searching for the “missing dot”—identifying the opposite direction to which the arrow was pointing—such a strategy

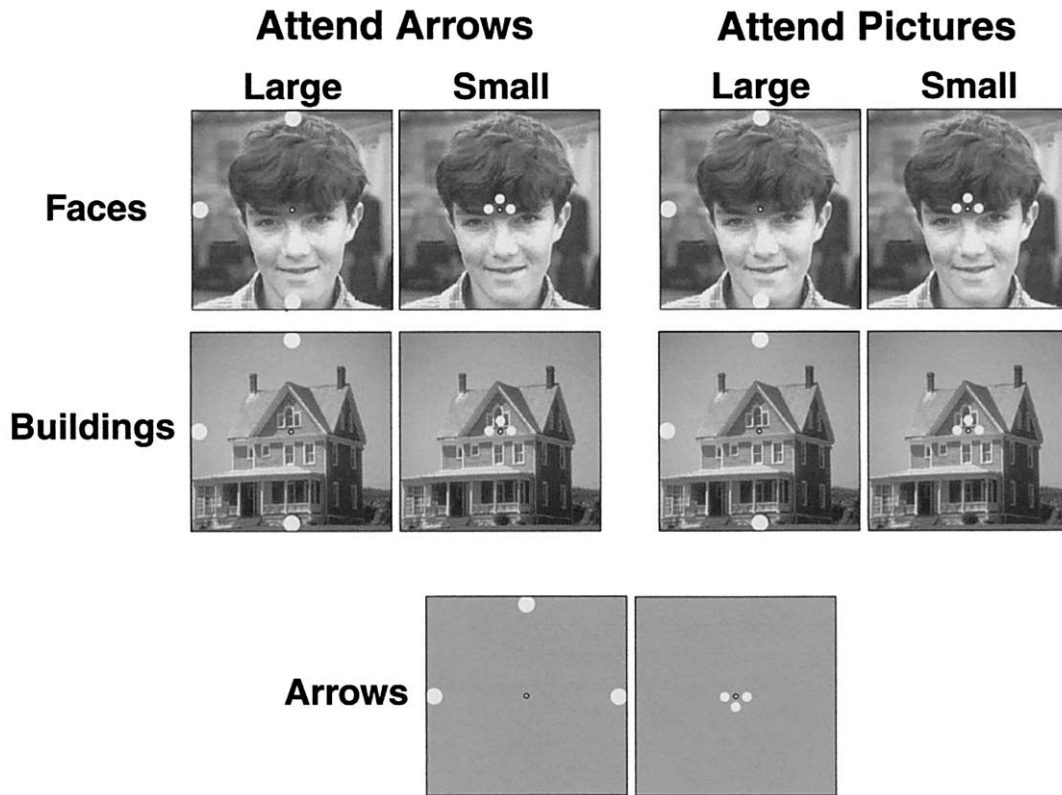


Fig. 1. Experimental design of attention experiment. Stimuli were presented in short epochs and included faces and buildings. A subjective arrowhead (either small or large), which was composed of 3 dots, was superimposed on each image. Dots were enlarged here for demonstration purpose and were red in the original experiment. Subjects were instructed to covertly name the arrow's direction in one set of epochs (attend arrows, left) and to perform a categorization task in the other set (attend pictures, right) while maintaining fixation throughout the experiment. Identical stimuli were presented in the two sets of epochs. The arrows also appeared alone during a separate condition.

would necessitate integrating information from all three dots.

Different epochs contained either small or large arrows. In each image the arrow was pointing randomly to one of the four cardinal directions with a small jitter. Additionally, the arrowheads (either small or large) appeared alone in two conditions, which were each repeated twice. A small (0.3×0.3 degrees) fixation-cross appeared in the middle of all images throughout the experiment.

Subjects were instructed to fixate on the fixation cross, located in the middle of each stimulus, and to attend either the object stimuli or the arrows. Instructions were conveyed by an image of a letter, which preceded each stimulus epoch and appeared for 2 s, the letters were F, H, or A. "F" indicated that the epoch would contain faces and that the subjects should attend the faces and covertly categorize each of them as female or male. "H" indicated that the epoch would contain buildings (houses) and that subjects should categorize each of them as a private or a public facility; in the following text we will refer to either of these conditions as "attend pictures." In contrast, the letter "A" indicated that subjects had to attend the superimposed arrow and to indicate the direction to which it pointed. Each of these conditions was repeated three times. Task perfor-

mance was verified for each subject during a training session performed outside the scanner on a different set of images. For five subjects performance of the original experiment was measured under similar experimental conditions, but outside the scanner, at least 2 months after the

Table 1
Behavioral data of attention experiment^a

Experimental condition	Proportion of correct responses	Reaction time (ms)
Faces large arrow, attend faces	0.90 ± 0.06	615 ± 57
Faces large arrow, attend arrows	0.98 ± 0.03	667 ± 49
Faces small arrow, attend faces	0.96 ± 0.03	611 ± 64
Faces small arrow, attend arrows	0.95 ± 0.03	641 ± 70
Houses large arrow, attend houses	0.82 ± 0.11	680 ± 47
Houses large arrow, attend arrows	0.99 ± 0.02	660 ± 52
Houses small arrow, attend houses	0.81 ± 0.09	642 ± 71
Houses small arrow, attend arrows	0.99 ± 0.02	619 ± 88
Large arrows alone	0.99 ± 0.03	583 ± 72
Small arrows alone	1.00 ± 0.00	527 ± 48

^a Proportion of correct responses and reaction times for each experimental condition of the attention experiment averaged across 5 subjects as measured outside the scanner. Values represent the mean ± SD. (See Results section for statistical analysis of the behavioral data.)

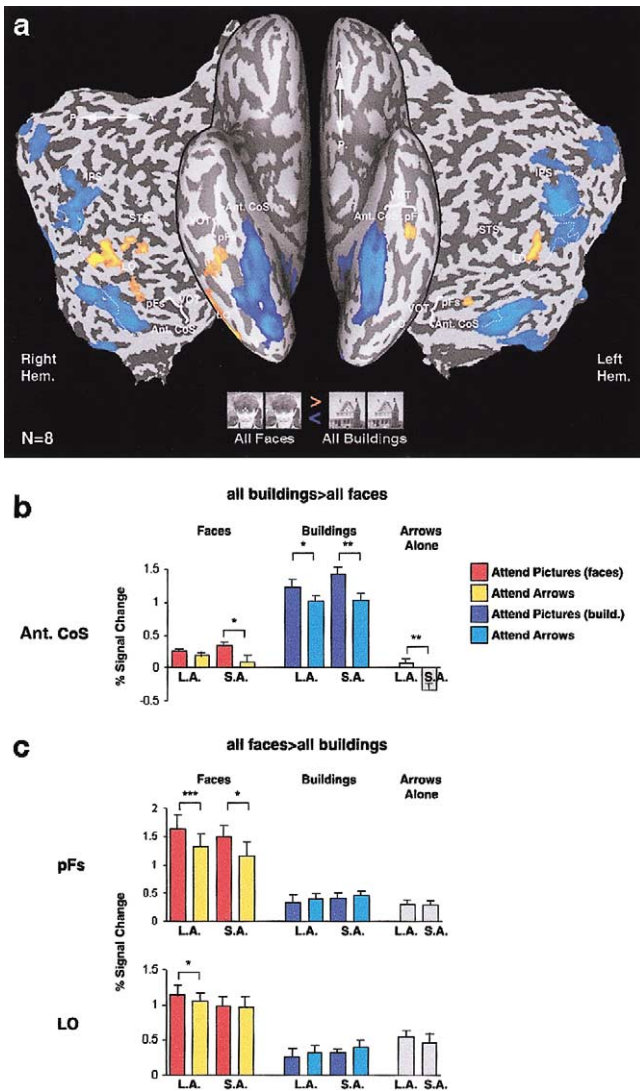


Fig. 2. Functional activation maps and activation profiles of regions of interest (ROIs). (a) Averaged activation map of the face and building-related activation (8 subjects, general linear model, GLM statistics) presented on two inflated hemispheres, shown from a ventral view and two unfolded hemispheres, of one subject. The white dotted line represents the estimated border between retinotopic (e.g., left of the white dotted line on the right hemisphere) and nonretinotopic (e.g., right of the white dotted line on the right hemisphere) visual areas. The map was created by applying two statistical tests, i.e., all faces > all buildings (orange) and all buildings > all faces (blue). Note that these tests were performed regardless of the attentional task. Regions of interest were defined by their preferential activation to either faces (LO and pFs), or buildings (Ant. CoS) and were restricted to nonretinotopic areas. Abbreviations: LO, lateral occipital; pFs, posterior fusiform; Ant. CoS, anterior collateral sulcus; VOT, ventral occipitotemporal; IPS, intraparietal sulcus; STS, superior temporal sulcus; A, anterior; P, posterior. (b) Activation profile of the collateral sulcus obtained by searching for building selective voxels (all buildings > all faces). Red, blue, and gray indicates the stimulus category, i.e., faces, buildings, and arrows-alone, respectively. Dark and light colors indicate the task performed by the subjects i.e., "attend pictures" or "attend arrows," respectively. Attentional modulation is manifested in a stronger signal during the attend-pictures compared to the attend-arrows condition. This region exhibited attentional modulation for the building stimuli for both arrow sizes and also substantial modulation for the face stimuli in the small-arrow condition. Asterisks denote significance level as calculated

original scan, so that priming effects would be avoided. Subjects provided their responses via a keyboard and responses were collected by in-house software. For each subject both mean reaction time and the proportion of correct responses were calculated for each experimental condition (Table 1).

Data analysis

Functional magnetic resonance imaging (fMRI) data were analyzed with the BrainVoyager software package (Brain Innovation, Maastricht, Netherlands) and with complementary in-house software. The cortical surface of each subject was reconstructed from the 3D-spoiled gradient echo scan. The procedure included segmentation of the white matter using a grow-region function, the smooth covering of a sphere around the segmented region, and the expansion of the reconstructed white matter into the gray matter. The sulci were smoothed using a cortical "inflation" procedure. The surface was cut along the calcarine sulcus and unfolded into the flattened format. The obtained activation maps were superimposed on the unfolded cortex and the Talairach coordinates (Talairach and Tournoux, 1988) were determined for the center of each ROI (region of interest). Preprocessing of functional scans included 3D-motion correction and filtering out of low frequencies up to 5 cycles per experiment (slow drift).

Statistical analysis was based on the general linear model (GLM) (Friston et al., 1995). The GLM analysis was performed independently for the time course of each individual voxel for each subject. Each experimental condition (except for blank) was defined as a separate predictor. The first three images of each functional scan were discarded, a boxcar shape was used for each predictor, and a hemodynamic lag of 3 s was assumed.

Percent signal change (PSC) for each subject was calculated as the percent activation from a blank baseline:

$$\text{Percent signal} = \frac{\text{signal} - \text{mean}[\text{signal}(\text{blanks})]}{\text{mean}[\text{signal}(\text{blanks})]} \times 100$$

Multisubject analysis

In addition to subject-by-subject analysis (Fig. 2b and c) we also analyzed the data in a multisubject approach (Figs. 2a, 3, 4, and 5). To obtain the multisubject maps, time series

between the attend-pictures and the attend-arrows conditions in each of the picture conditions, or between the large- and small-arrow conditions when they were presented alone (paired *t* test, **P* < 0.05, ***P* < 0.005, ****P* < 0.0005), error bars indicate \pm standard error of the mean (SEM). Abbreviations: L.A., large arrow, S.A., small arrow. (c) Activation profiles of areas pFs (top) and LO (bottom) obtained by searching for face-selective voxels (all faces > all buildings). Note that pFs exhibited significant attentional modulation for the face stimuli for both arrow sizes, while LO exhibited this effect only for the large-arrow condition. Conventions as in Fig. 2b.

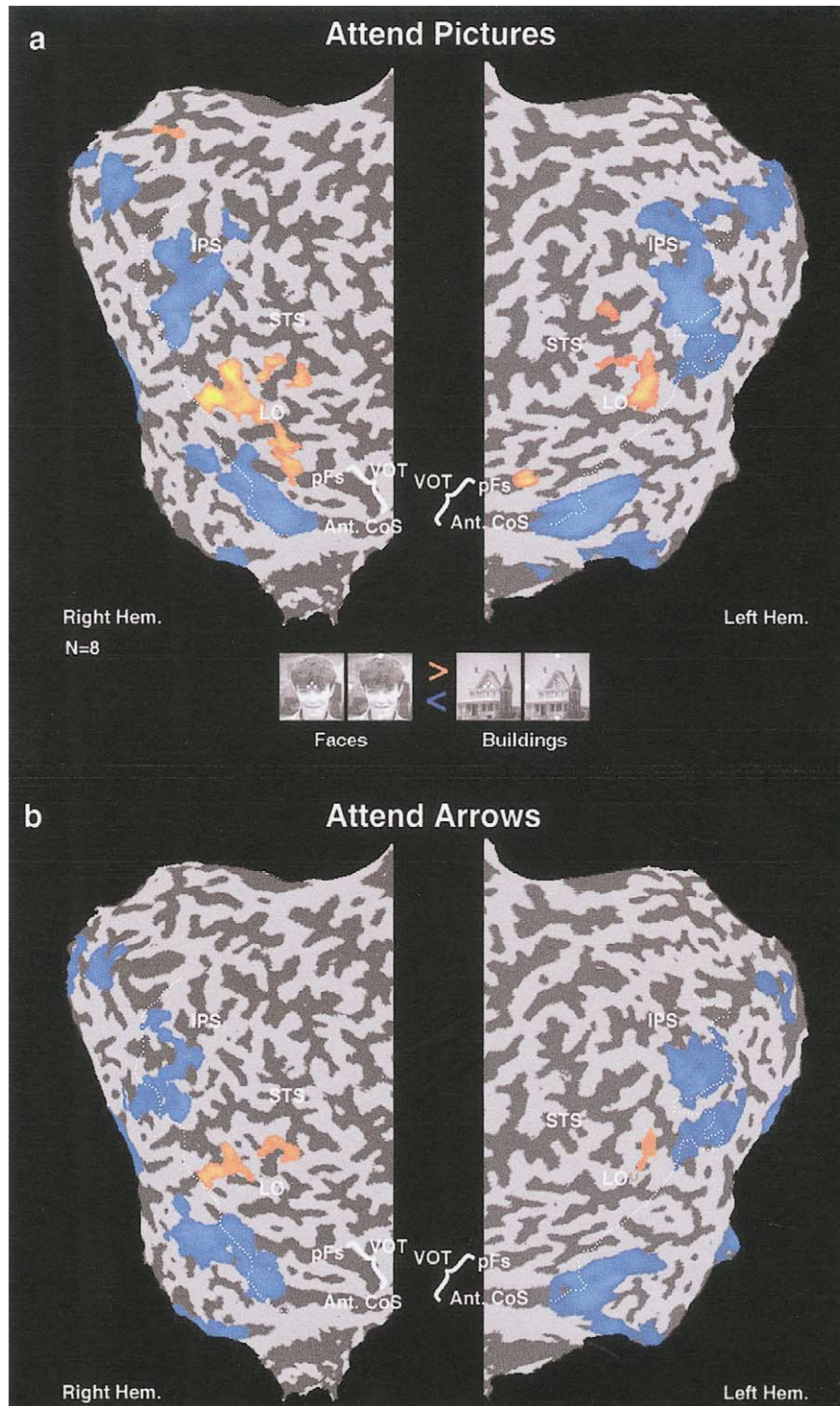


Fig. 3. Stimulus selectivity maps under different attentional states. (a) Stimulus selectivity maps of the “attend pictures” conditions. Averaged activation maps of stimulus selectivity (8 subjects, general linear model, GLM, statistics) presented on two unfolded hemispheres of one subject. The map was created by applying two statistical tests contrasting the faces (orange) and buildings (blue) while subjects were attending these stimuli. Note the strong face selectivity within face-related LO and the pFs and the strong building selectivity within the Ant. CoS. (b) Stimulus selectivity maps of the “attend arrows” conditions. Same maps as in Fig. 3a but created by contrasting the faces and buildings stimuli during the attend-arrows condition. Note that the stimulus selectivity in occipitotemporal regions was largely maintained across the two different attentional states (Fig. 3a vs. Fig. 3b). However, activity during the attend-pictures condition was extended into more anterior regions, and particularly into the pFs region. Abbreviations same as in legend to Fig. 2.

of images of brain volumes were converted into Talairach space, z -normalized and concatenated. The statistical tests were performed on the concatenated time course. In the

relevant figures, the multisubject functional maps are projected on the inflated and flattened Talairach normalized brain of one subject. Significance levels of the averaged

activation maps presented in the study were calculated taking into account the minimum cluster size and the probability threshold of a false detection of any given cluster (Forman et al., 1995). This calculation was accomplished by a Monte Carlo simulation [AlphaSim software by B. Douglas Ward, which is part of the AFNI analysis package (Cox R. W., 1996)]. Specifically, the probability of a false positive detection per image was determined from the frequency count of cluster sizes within the entire cortical surface (not including white matter and subnuclei) using the combination of individual voxel probability thresholding and a minimum cluster size.

For Figs. 2a, 3, and 4a the statistical significance was $P < 5 \times 10^{-4}$. The minimum cluster size used for creating Figs. 2a and 3 was 6 contiguous voxels, while in Fig. 4a, a cluster size of 9 contiguous voxels was used to reach the same level of statistical significance. In the map shown in Fig. 5a, the statistical significance was $P < 5 \times 10^{-6}$ and the cluster size was again limited to 6 contiguous voxels.

For creating the two-color map presented in Fig. 5a, the GLM model was recalculated using a subset of the predictors (Faces, attend large arrows, and Buildings, attend small arrows). The highlighted voxels in the figure are those for which this reduced model explained a substantial portion of the variance ($P < 5 \times 10^{-6}$). When mapping the relative contribution of two functional responses, the color coding represents the relative contribution of either set. If both predictor sets contribute roughly equally at a voxel, yellow color will be seen. If the first predictor set contributes strongly whereas the other does not, red to orange colors will be seen. If the second predictor set contributes strongly but not the first, dark to light green colors will be seen. The exact color used depends on the strength of asymmetry between the contributions. In Fig. 5a red represents exclusive contribution of the first predictor set (Faces, attend large arrows) while dark green represents exclusive contribution of the second predictor set over the other (Buildings, attend small arrows).

Results

The aim of the experiment was to examine both spatial and object-based attentional modulation effects within face- and building-related regions. During the experiment, subjects viewed an identical set of visual stimuli that consisted of complex natural objects (either faces or buildings) with superimposed 3-dot sets, forming either a small or a large subjective arrow-head (Fig. 1). Subjects were instructed to attend to different aspects of the stimuli during different epochs. In one case, the subjects attended the pictures of either the faces or buildings (in the text we will refer to this condition as “attend pictures”) and in the other they attended the arrows (small or large) (see Materials and Methods for more details).

Averaged proportion of correct responses and of reaction

Table 2
Talairach coordinates^a

	Left			Right		
	X	Y	Z	X	Y	Z
LO	-47 ± 4	-69 ± 6	-6 ± 4	43 ± 5	-62 ± 7	-4 ± 5
pFs	-38 ± 2	-48 ± 9	-15 ± 5	34 ± 6	-44 ± 4	-15 ± 4
Ant. CoS	-25 ± 2	-46 ± 8	-9 ± 5	23 ± 4	-42 ± 3	-8 ± 3

^a Talairach coordinates (Talairach and Tournoux, 1988) for LO, pFs, and Ant. CoS derived from all subjects. Values represent the mean ± SD in millimeters (mm). LO, lateral occipital region; pFs, posterior fusiform region; Ant. CoS, anterior collateral sulcus.

times for this task, as measured for five subjects outside the scanner but under similar viewing conditions, are given in Table 1. Performance as measured by proportion of correct responses was generally high during all experimental conditions. Note specifically the high performance during all the “attend arrow” conditions, which implies that subjects’ attention was indeed engaged by that task. A three-way analysis of variance (ANOVA) using the stimulus category, arrow size, and attentional task as the main effects was calculated across all experimental conditions except for the “arrows alone” conditions. This analysis revealed a significant main effect of stimulus category ($F = 5.3$, $P < 0.05$), and of attentional task ($F = 35.0$, $P < 10^{-4}$) as well as a significant interaction between these two factors ($F = 14.1$, $P < 10^{-3}$) in the proportion of correct responses data. Thus, indicating that performance of the building task was significantly lower than performance of the face task. However, a similar analysis of the averaged reaction time did not reveal any significant effect.

We first looked at the general attention effect within three nonretinotopic high-order object-related ROIs: the anterior collateral sulcus (Ant. CoS), posterior fusiform region (pFs), and the lateral occipital region (LO). The Ant. CoS was defined by its preferential activation to buildings compared to faces regardless of the attentional demands (all buildings > all faces). pFs and LO were defined by their preferential activation to faces compared to buildings (all faces > all buildings) and separated according to anatomical criteria. The former focus was situated in the vicinity of the posterior fusiform gyrus (pFs), which is anterior and lateral to area V4/V8 and extended into the inferior temporal sulcus and the latter (LO) was situated ventrally and posteriorly to area MT/V5 and extended into the posterior inferotemporal sulcus. The posterior fusiform region (pFs) and the anterior part of the collateral sulcus (Ant. CoS) compose the ventral occipito-temporal cortex (VOT) (Malach et al., 2002).

Each ROI was defined separately for each subject (see Table 2 for Talairach coordinates of each region). Fig. 2a shows a functional map of these ROIs as averaged across all eight subjects; data are shown on two inflated and unfolded hemispheres. The white dotted line, marked on both unfolded hemispheres, is an estimated border separating ob-

ject-related regions from lower visual areas. This border was obtained by contrasting objects vs. texture patterns in a separate localizer experiment that was run during a different scanning session. Details of this experiment can be found in the study by Levy et al., (2001). This was done for 7 of 8 subjects.

To obtain a quantitative measure of the activity level during the different experimental conditions we performed time course analysis for each subject in each of the ROIs. To relate to the attentional modulation in each of these ROIs, we compared the activity during epochs that were identical in terms of their physical content but differed in terms of the task performed by the subjects (i.e., attending the pictures vs. attending the arrows). Statistical significance was verified by a paired *t* test calculated between the attend-pictures and attend-arrows conditions, for each arrow size in each ROI. The results of this analysis are shown in Fig. 2 b and c.

Fig. 2b shows the activation profile of the building-related region in the anterior collateral sulcus (Ant. CoS). This region exhibited significant signal enhancement when attending the building images compared to the arrows for both the large- and small-arrows conditions. In addition, this region also exhibited a significantly greater fMRI signal (PSC) for the large arrows compared to the small arrows when presented alone (paired *t* test), and during the face-images condition, a slight preferential activation for attending faces vs. attending the small arrows.

Fig. 2c shows the activation profile of face-related regions within the pFs and LO. Note that despite the similarity in the face selectivity in both pFs and LO, two differences were evident in the activation profile in these two regions. First, pFs exhibited substantial signal enhancement when attending the face stimuli, while LO exhibited a weaker level of such modulation, which was evident only for the large-arrow condition. Second, LO exhibited stronger activation than the pFs for the arrows-alone condition both for the large and small arrows (two-way ANOVA: significant main effect of ROI: $F = 5.2$, $P < 10^{-2}$; but no effect of arrow size: $F = 0.4$, $P < 0.6$; and no significant interaction between these factors: $F = 0.03$, $P < 0.9$).

To what extent was the differential activation to buildings and faces dependent on the specific type of attention? To examine this issue we directly compared the activation maps obtained from epochs in which attention was directed to the building or face images, with maps obtained when subjects attended the arrows superimposed on these images. Fig. 3 shows the results of this comparison. Importantly, these two sets of epochs were physically identical, and differed only in terms of the task performed by the subjects. Fig. 3a was obtained by comparing the activation to face images (orange) with the activation to buildings (blue) when subjects attended the pictures of objects. Fig. 3b was obtained by applying the same test, and using the same statistical threshold in the epochs in which subjects attended the arrows.

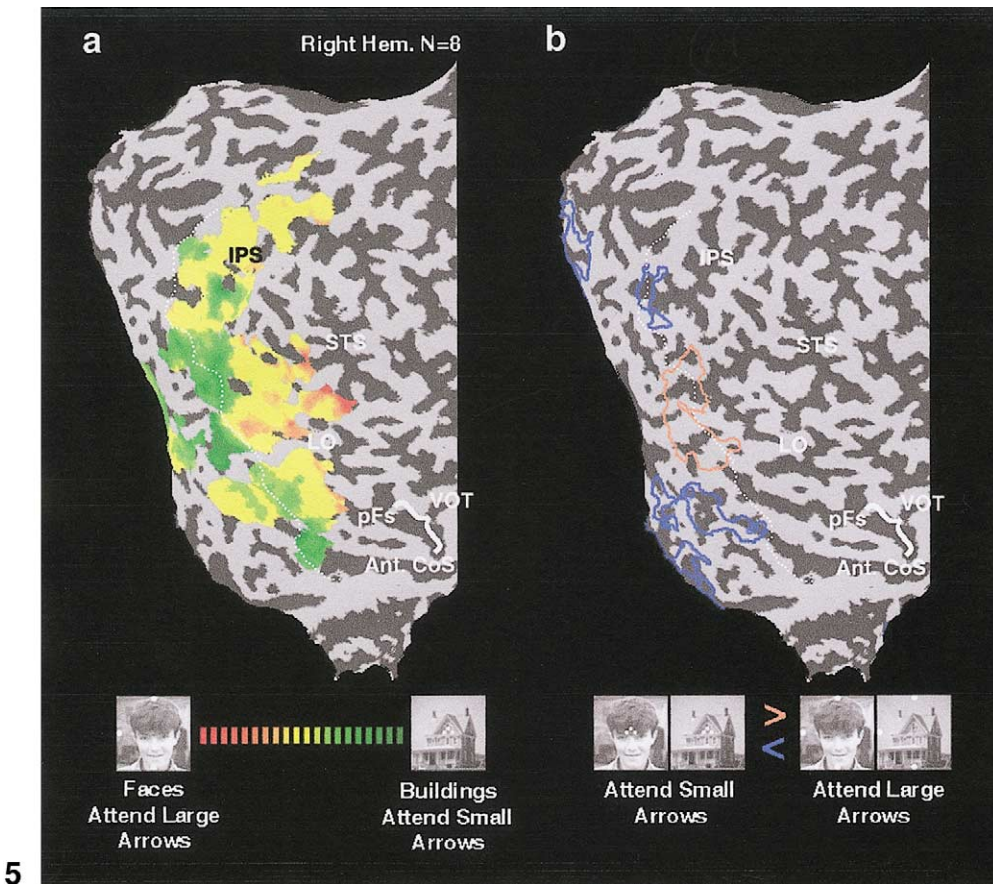
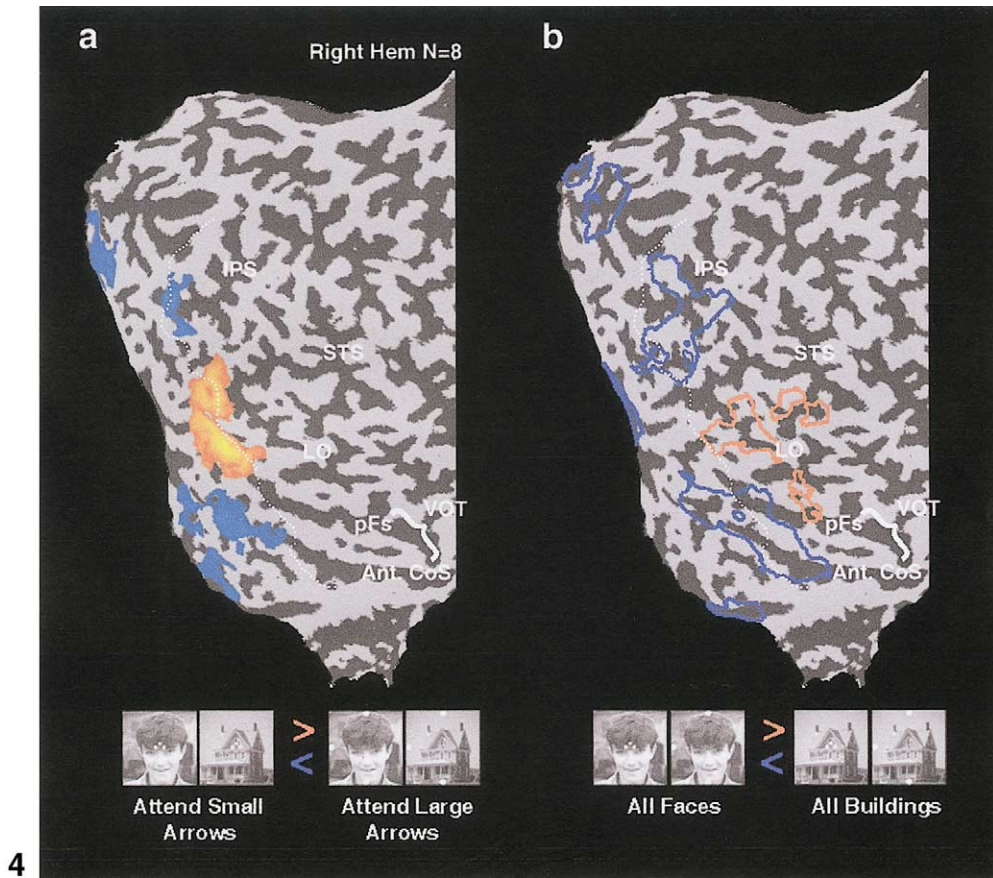
Generally, the differential activation to buildings and

faces in occipitotemporal regions were maintained during both attentional states; however, some differences between these two conditions were still found. First, the activation in the Ant. CoS was enhanced and extended toward more anterior regions, when subjects attended the building pictures (Fig. 3a). However, performance of the building task was apparently more difficult than the other tasks (significantly poorer performance, Table 1) so it could be that task difficulty also contributed to some extent to this building-related activation (Fig. 3a). Second, face-related activation within pFs was absent when subjects attended the arrows (however, it could be observed at a lower statistical threshold in this region) and face-related activation within LO was also weaker under these conditions. Importantly, careful analysis (not shown) revealed that the spread of the activation obtained in the attend-pictures condition in all ROIs was confined to the anterior direction and did not extend sideways, thus making it unlikely that this extension was simply due to higher activation level obtained in this condition.

Thus, our results show that while shape-related selectivity in LO and VOT was not fully dependent on attention to specific shapes, it could be substantially intensified by it.

We next examined the extent to which manipulating spatial (“spotlight”) attention while keeping the face and building shapes constant could differentially affect VOT and LO activation. This was done by comparing the activation during all the conditions in which subjects attended the large arrows (blue) vs. the conditions in which they attended the small arrows (orange). The conditions in which the arrows appeared alone were not included in the statistical analysis. Note, however, that this comparison involves a slight change in the physical properties of the stimulus (i.e., small vs. large arrows).

The results of this analysis are shown in Fig. 4a. To enable comparison, Fig. 4b shows the contours of the three different ROIs that were presented in Fig. 2a. Note that the retinotopic areas (e.g., left of the dotted white line on the right hemisphere) showed a clear attention-related eccentricity map; that is, center visual field representations were activated more strongly when attention was directed to the small foveal arrows (orange), while peripheral visual field representations were preferentially activated by attention to the large peripheral arrows (blue). Importantly, this attentional eccentricity map extended slightly outside the retinotopic areas (right of the white dotted line) into the vicinity of LO where some central-related activation was obtained but did not extend into VOT. Note that there was almost no overlap between activity in high-order nonretinotopic object-related areas as shown on Fig. 4b and the attention-related eccentricity map (Fig. 4a). Importantly, the same findings were maintained even when the statistical threshold was substantially reduced (data not shown). These results indicate that activity in these regions was not substantially modulated by spatial shifts in attention when attention was directed to the arrow shapes.



Given the central bias found in face-related regions and the peripheral bias found in building-related regions (Levy et al., 2001), a critical test for assessing the effect of spatial attention on the activation in these regions would be to compare the activation for each of these object categories while attention is directed to their nonpreferred eccentricity. We therefore compared the activation during epochs containing faces and large arrows in which subjects attended the arrows (red in Fig. 5a) and epochs containing buildings and small arrows in which subjects attended the arrows (green). If the source of the category-related activation in LO and VOT is the size of the attentional spotlight then we would expect that face-related regions would be strongly activated by attending the small arrows superimposed on the building images and building-related regions would be strongly activated by the large arrows superimposed on the face images.

The results of this test are shown in Fig. 5a; for comparison, the contours of the attention-related eccentricity map from Fig. 4a are given in Fig. 5b. Interestingly, while retinotopic areas (left of the white dotted line) particularly within the center-biased regions tended to be activated according to the attended eccentricity (that is, small vs. large arrows), the effect was reversed within high-order object-related areas (right of the white dotted line). Thus, face-related LO and pFs tended to be more strongly activated by the face stimuli as evident from the red color assigned to them, despite that attention was directed to the large peripheral arrow. In contrast, the building-related Ant. CoS tended to be strongly activated by the building stimuli as evident by the dark green color assigned to it, despite that spatial attention was actually directed to the small central arrow.

Finally, if space-based attention was indeed a dominant factor in determining the activation in the high-order face- and building-related regions we would expect that the selectivity for these object shapes would be modulated when spotlight size changes. In other words we would expect to find significant interaction between object shape and spotlight size in these regions when subjects were attending the arrows. To directly test this prediction we performed a two-way ANOVA analysis on the time courses sampled from each subject from each of the three ROIs shown in Fig.

2 (i.e., Ant. CoS, pFs, and LO) during the attend-arrows conditions. In this analysis, object shape (faces and buildings) and arrow size (small and large) were defined as the main effects and we were specifically looking for the interaction between these two factors. Note that the ROIs were defined solely by their building and face selectivity and therefore their time courses were not biased by either attentional demands or arrow size. Interestingly, this analysis failed to show a significant interaction between object shape and arrow size in all ROIs (in all ROIs: $F = 0.50$, $P < 0.5$ for the interaction term, object shape \times arrow size), thus demonstrating that the selectivity for faces and buildings when attending the arrows was not affected by the size of the attentional spotlight (i.e., arrow size). This finding was further confirmed by an additional analysis of the data set using a similar two-way ANOVA model and directly searching for voxels significantly activated by the interaction term. Critically, no such statistically significant activation was found.

Taken together, these results clearly indicate that object identity rather than spatial attention effects are the critical factor in determining the activation in high-order object-related areas.

Discussion

Interaction between eccentricity mapping and attentional modulation

Recently, we have found evidence for topography organization according to eccentricity bias that extends beyond the classical retinotopic areas into high-order ventral stream visual areas (Levy et al., 2001; Malach et al., 2002). In addition, we have shown a clear association between category-specific activation and eccentricity. The present results are relevant to the question of how the eccentricity biases in occipitotemporal cortex emerge. One can envision several different alternatives: it could be that the association between category-related activation and eccentricity was created due to slow ecological needs imposed during evolution, and therefore this association is now innate or hardwired.

Fig. 4. Attention-related eccentricity mapping. (a) Averaged attention-related eccentricity map (8 subjects, general linear model, GLM, statistics) presented on a right unfolded cortical hemisphere. The map was obtained by applying two statistical tests; i.e., the first test contrasted the conditions in which subjects attended the small arrows with the conditions in which they attended the large arrows (orange), across the face and building stimuli; the second test was the opposite test (blue). A clear attention-related eccentricity map was obtained within a lower, retinotopic visual area (left of the white dotted line on the right hemisphere). This map (central representation) slightly extended into the more dorsal lateral occipital (LO) area but not into VOT (right of the white dotted line). (b) Contours of the building- and face-related regions of interest that were presented in Fig. 2a are shown on the unfolded right hemisphere to enable direct comparison between the location of the attention-related eccentricity activation and the location of the object-related regions of interest.

Fig. 5. Posterior to anterior transition from visual field to object sensitivity. (a) Averaged map (8 subjects, general linear model, GLM, statistics) presented on one right, unfolded cortical hemisphere. The map was obtained by applying a statistical test comparing the activation during epochs in which subjects attended large arrows superimposed on face images (red) to the conditions in which they attended small arrows superimposed on building images (green). Areas that showed a more balanced activation to both conditions are color-coded in yellow. Note that while retinotopic visual areas (left of the white dotted line) were generally activated according to the attention to visual field eccentricity imposed by the arrowhead size, nonretinotopic object-related areas (right of the white dotted line) were activated according to their object preferences. (b) Contours of the attention-related eccentricity map taken from Fig. 4a are shown on the unfolded right hemisphere to enable comparison between the two sets of results.

Alternatively, it could be that such needs are imposed during development, so that this association is being acquired rather than innate. Compatible with this notion are findings showing that representations within high-order object-related areas can be modified following learning (Gauthier et al., 1999) and also findings showing that written letter strings and words preferentially activate regions that are associated with central representations (Hasson et al., 2002).

Finally, it could be that the eccentricity-category association is not a result of any long-term processes but rather is a result of real-time spatial attentional shifts. According to this alternative, whenever one encounters a stimulus, which requires high-acuity demands (e.g., a face or a word), a small central “spotlight of attention” is used and hence visual areas, which have a central bias, are immediately recruited. In contrast, whenever stimuli that require large-scale feature integration are presented (e.g., buildings), one uses a large, peripheral spotlight of attention and this recruits areas, which are associated with peripheral field representation.

Spotlight attention effects were indeed discovered in retinotopic visual areas (Brefczynski and DeYoe, 1999; Martinez et al., 1999; Somers et al., 1999; Tootell et al., 1998) and also in high-order object-related areas (Downing et al., 2001). Moreover, increased activity was found in retinotopic visual areas when subjects directed their attention to particular location in a visual scene even in the absence of a visual stimulus (Kastner et al., 1999)

Thus, if the source of the eccentricity-category association was due to shape-independent spatial attention, then in the current experiment we would expect to find that whenever subjects attended the small arrows, central-biased regions would be recruited regardless of the identity of the underlying stimulus (i.e., a face or a building) while peripheral regions would be activated when attending the large peripheral arrow. However, the results show that shape selectivity maps within VOT (pFs and the Ant. CoS) as well as within LO were largely maintained regardless of the attentional task (i.e., attention to pictures in Fig. 3a compared to attention to arrows in Fig. 3b) or the spatial focus (Fig. 5a); moreover, the selectivity for faces and buildings was not affected by changing the spotlight size. One possible exception for this conclusion was observed in the Ant. CoS, where large arrows, when presented alone, produced a significantly higher activation than the small arrows (Fig. 2b); however, this effect may also be due to a greater spatial integration involved in the large-arrow condition. This general preservation of the stimulus selectivity maps under different attentional states show that shape-invariant space-based attentional demands could not account for the category-topography association found in high-order object-related areas.

On the other hand, shifting attention from the arrows to the face/building pictures enhanced the activation in the VOT and extended this activation further anteriorly (compare Fig. 3a and b). This modulatory effect provides further

support for the existence of object-based attentional mechanism (Desimone and Duncan, 1995; Duncan 1984; Vecera and Farah, 1994) within those areas. Such object-based attentional modulations were shown by O’craven et al., (1999) in the fusiform face area, (FFA; Kanwisher et al., 1997), and in the parahippocampal place area (PPA; Epstein and Kanwisher 1998), when stimuli (faces and buildings) occupied the same location in space.

The fact that VOT activation extended further anteriorly during selective attention to pictures of objects is nicely compatible with the notion of a posterior-anterior hierarchical axis of object representation (Avidan et al., 2002; Lerner et al., 2001). Thus, it appears that the anterior part of the VOT further departs from the physical retinal stimulus and is more tightly coupled to the perceptual or attentional state of the observer compared to its posterior part.

A combined attentional effect

In the present study we found that while the eccentricity-related attentional effects extended slightly into LO, the VOT itself was largely unaffected by such spatial attention effects. This result can be explained by the fact that VOT was not sensitive to the arrow shapes (see Ant. CoS and pFs, Fig. 2b and c, respectively).

Taken together, the results are compatible with an organization principle of occipitotemporal object-related cortex, which can be described as a combination of two selectivity dimensions, i.e., sensitivity to object shape, on the one hand, and the eccentricity map, on the other hand (Levy et al., 2001; Malach et al., 2002). Similarly, attentional modulation in these regions appears to require both shape selectivity and eccentricity. From this analysis we can hypothesize that attending to a combination of object shape and eccentricity, i.e., attending to face images in the visual field center vs. its periphery, may reveal stronger eccentricity-bias attentional effects in the VOT.

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