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Equal Degrees of Object Selectivity for Upper and Lower Visual Field Stimuli

Lars Strother, Adrian Aldcroft, Cheryl Lavell, and Tutis Vilis
Department of Physiology and Pharmacology, Canadian Institutes of Health Research Group for Action and Perception, University of Western Ontario, Ontario, Canada

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Strother L, Aldcroft A, Lavell C, Vilis T. Equal degrees of object selectivity for upper and lower visual field stimuli. *J Neurophysiol* 104: 2075–2081, 2010. First published August 18, 2010; doi:10.1152/jn.00462.2010. Functional MRI (fMRI) studies of the human object recognition system commonly identify object-selective cortical regions by comparing blood oxygen level–dependent (BOLD) responses to objects versus those to scrambled objects. Object selectivity distinguishes human lateral occipital cortex (LO) from earlier visual areas. Recent studies suggest that, in addition to being object selective, LO is retinotopically organized; LO represents both object and location information. Although LO responses to objects have been shown to depend on location, it is not known whether responses to scrambled objects vary similarly. This is important because it would suggest that the degree of object selectivity in LO does not vary with retinal stimulus position. We used a conventional functional localizer to identify human visual area LO by comparing BOLD responses to objects versus scrambled objects presented to either the upper (UVF) or lower (LVF) visual field. In agreement with recent findings, we found evidence of position-dependent responses to objects. However, we observed the same degree of position dependence for scrambled objects and thus object selectivity did not differ for UVF and LVF stimuli. We conclude that, in terms of BOLD response, LO discriminates objects from non-objects equally well in either visual field location, despite stronger responses to objects in the LVF.

INTRODUCTION

The ventral visual pathway is thought to be crucial for object perception and recognition (Logothetis and Sheinberg 1996; Tanaka 1996). Within this pathway, the human lateral occipital visual area (LO) lies amidst of a hierarchy of cortical areas extending anteriorly and ventrally from primary visual cortex (Malach et al. 1995). It is well known that LO is object selective in that it produces stronger neural responses to objects than other non-object stimuli. This defining characteristic of LO has been shown in numerous studies using functional MRI (fMRI) and a variety of visual stimuli (Grill-Spector et al. 1998, 2000; Hasson et al. 2002; Kourtzi and Kanwisher 2000; Lerner et al. 2001; Levy et al. 2001; Malach et al. 1995, 2002).

Whereas object selectivity in LO is well established, the role of LO in object recognition is not known, although fMRI activity in LO has been shown to correlate with recognition performance (Grill-Spector et al. 2000). One commonly assumed characteristic of a successful position-invariant object recognition system is that it should be able to categorize an object irrespective of changes in the location and orientation of an object with respect to the eye (Edelman and Poggio 1991; but see Kravitz et al. 2008). Thus a related and currently outstanding question concerning LO is whether its ability to discern objects from non-objects (e.g., in terms of fMRI response magnitude for objects and scrambled objects) varies with retinal stimulus location. Although LO has been shown to represent fairly precise spatial location information (Larsson and Heeger 2006; Sayres and Grill-Spector 2008; Schwarzlose et al. 2008), the possibility that the degree of object selectivity in LO might depend on retinal stimulus location has not been examined.

Perhaps the most compelling evidence that LO represents detailed information about stimulus location comes from Larsson and Heeger (2006). They reported two new retinotopic maps in human lateral occipital cortex (LO1 and LO2, both defined exclusively on the basis of retinotopy produced by checkerboard patterns), one of which seemed to overlap with area LO (conventionally defined as a region of maximal object-selectivity in lateral occipital cortex). The findings of Larsson and Heeger offer a substantial advance over studies that previously suggested only a coarse representation of visual field location in ventral visual cortex (Grill-Spector et al. 1998; Levy et al. 2001; McKyton and Zohary 2007; Niemeier et al. 2005; Tootell and Hadjikhani 2001; Tyler et al. 2005). Consistent with the findings of Larsson and Heeger (2006), Sayres and Grill-Spector (2008) also reported reliable retinotopic maps in lateral occipital cortex and confirmed that one of these maps overlapped with LO. Crucially, Sayres and Grill-Spector conducted an additional experiment to assess the relation between object selectivity in LO and the sensitivity of LO to stimulus position suggested by their retinotopic maps. They presented different categories of objects (faces, animals, body parts, cars, sculptures, and houses) at different locations in the visual field. This protocol allowed them to evaluate whether LO responses to object stimuli were modulated by the position of the object. They found that LO responses to objects were strongly influenced by stimulus position, and their results were commensurate with retinotopic maps in LO obtained using non-object stimuli.

The findings of Sayres and Grill-Spector (2008; and also Schwarzlose et al. 2008) clearly showed that LO represents location information for both objects and non-objects. In addition to their retinotopic maps, they showed that LVF objects elicit greater neural responses than do UVF objects. However, Sayres and Grill-Spector did not examine whether the degree of object selectivity in LO for LVF-presented stimuli was greater than that for UVF stimuli. That is, although they used object selectivity to identify their LO regions of interest

Address for reprint requests and other correspondence: L. Strother, Univ. of Western Ontario, Dept. of Physiology and Pharmacology, Social Science Ctr., Rm. 6244, London, ON N6A 5C2, Canada (E-mail: lstroth@uwo.ca).

(ROIs), their methods did not enable them to examine whether LO responses to objects and non-objects would be equally modulated by stimulus location. We therefore presented observers with images of objects and scrambled versions of these images at different locations in the visual field to directly compare LO responses between the two stimulus categories at disparate peripheral locations on the retina. We also performed retinotopic mapping in some of our subjects and compared our results between the two experiments.

METHODS

Subjects

Fourteen healthy right-handed volunteers participated in *experiment 1* (8 male, 6 female; age, 21–40 yr), 10 of whom also participated in *experiment 2* (6 male, 4 female). One of the participants was the first author. All participants gave written consent, and all procedures were in accordance with and approved by the University of Western Ontario Ethics Review Board.

Stimuli

EXPERIMENT 1: OBJECT SELECTIVITY. We performed a variant of a conventional object-area (i.e., LO) localizer, originally reported by Malach et al. (1995) and used in numerous other studies. Observers fixated a small, centered, fixation dot (~0.5°) while presented with images of either line-drawn animals superimposed on an 8 × 8 grid (~3.5°) at a rate of 1 Hz or scrambled versions of these animals created by randomly shuffling the positions of each cell in the grid (Fig. 1*A*). We used a block design (12 s per block, with 36 blocks in each run; 6 blocks for each of the 6 conditions), where each block was presented at one of three locations (Fig. 1*A*). In one third of the blocks, images were presented at fixation; these blocks were used to define area LO (see ROI selection below). In the remaining two thirds of the blocks, images were presented either 7° above (UVF) or below (LVF) central fixation. To ensure alertness during the scans, observers performed a one-back task (i.e., pressed a key each time they saw an image repeat successively). Within each run, the blocks were presented in a random counter-balanced order, and we repeated each of these runs two to four times in each session.

EXPERIMENT 2: RETINOTOPIC MAPPING. Additionally, we performed a retinotopic mapping experiment identical to that reported by Sayres and Grill-Spector (2008), except that we only mapped the left visual field. Subjects were presented with a phase-reversing (temporal frequency = 2 Hz), 100% contrast-defined checkerboard wedge (with a spatial frequency of ~0.85 cycle/°). The wedge stimulus subtended 45° and extended 14° into the periphery (Fig. 1*B*). This wedge began at the 12 o'clock position (90° upright, UVF, apex at center screen) and rotated counterclockwise to the 6 o'clock position. The duration of each phase-reversing wedge was 2 s, after which the wedge location revolved counterclockwise around the center of the screen by 15° (resulting in 33% overlap between each wedge and its successor). At the end of each half-cycle (26 s), the wedge returned to the 12 o'clock position. Individual runs consisted of eight stimulus presentation cycles, each lasting 24 s. We performed one to three runs for each individual subject.

Functional and anatomical scans

The two experiments were performed using a 3-T Siemens Magnetom Tim Trio imaging system. In both experiments, blood oxygen level–dependent (BOLD) data were collected using T2*-weighted interleaved, single segment, echo-planar imaging (EPI), PAT = 2, and a 32-channel head coil (Siemens). In each experiment, the parameters for obtaining functional data were FOV = 240 mm × 240 mm; in-plane pixel size = 3 × 3 mm; TE = 30 ms; TR = 2,000 ms (single shot); volume acquisition time = 2 s; FA = 90°; 36 slices (slice thickness = 3 mm). Functional data were aligned to high-resolution anatomical images obtained using a 3D T1 MPRAGE sequence (TE = 2.98 ms; TR = 2,300 ms; TI = 900 ms; flip angle = 15°; 192 contiguous slices of 1.0 mm thickness; FOV = 192 × 256 mm^2).

Data analysis

Analyses of fMRI data were performed using Brain Voyager QX software. For both experiments, preprocessing of all functional data included head motion correction (scans with >1.5 mm estimated net motion were discarded), high-pass filtering, and linear trend removal. The two dimensional (2-D) functional images were aligned to 3-D anatomical data, and all were transformed into Talairach space (Talairach and Tournoux 1988). 3-D statistical maps were created for each subject based on contrasts within a general linear model.

ROI selection

In *experiment 1*, observers were presented with images of objects and scrambled objects presented either centrally (at fixation) or peripherally (in either the UVF or the LVF). The central fixation stimulus condition was equivalent to a conventional LO localizer. We therefore used this condition to define our ROI. Shown in Fig. 2*A*, LO was defined in individuals as a region that responds more strongly to images of objects than their scrambled counterparts ($P < 10^{-5}$, general linear model applied to each voxel). Note that we used only the data from the centrally presented stimulus condition to define LO (i.e., data

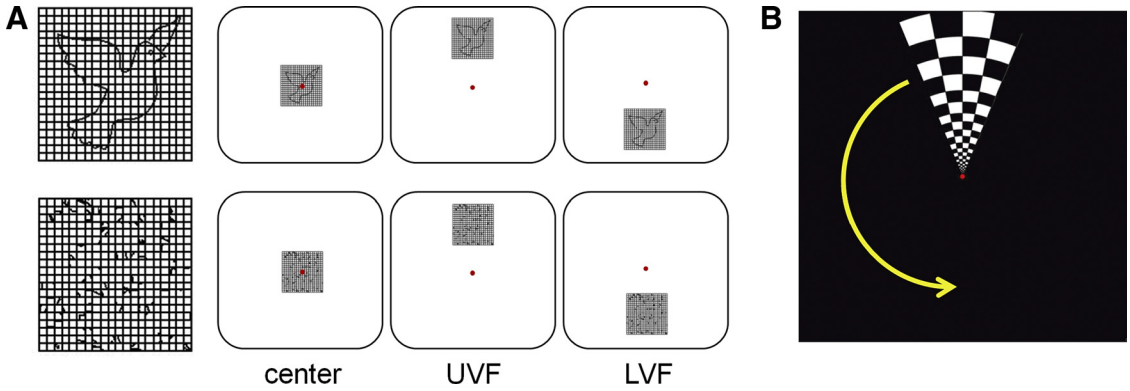

FIG. 1. Stimuli (not to scale) and conditions for *experiment 1* and *experiment 2*. *A*: in *experiment 1*, participants were shown images of objects (*top left*) and scrambled images (*bottom left*). These were displayed on the center of the screen or above [upper visual field (UVF)] or below [lower visual field (LVF)] fixation (remaining panels). *B*: in *experiment 2*, participants viewed 2-Hz contrast-reversing checkered wedges that rotated throughout the left visual field.

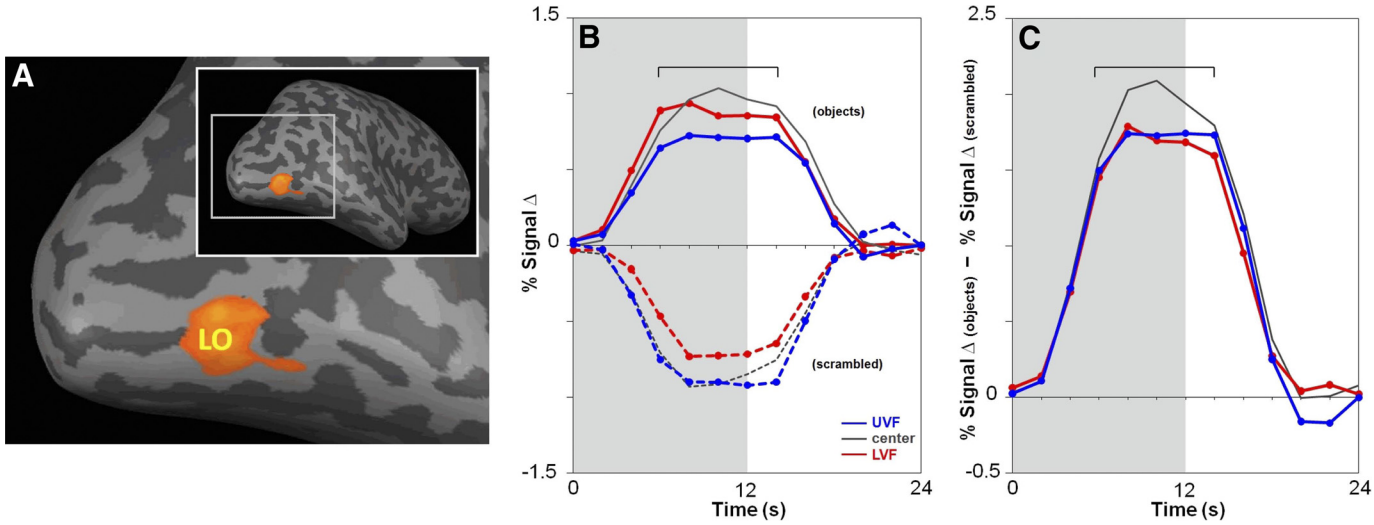

FIG. 2. *A*: 1 representative subject's object-selective region of interest (ROI), lateral occipital cortex (LO). This ROI responded more strongly to objects than the scrambled counterparts of these objects, both presented at central fixation. *B*: averaged functional MRI (fMRI) time course data for each of 6 experimental conditions for all subjects (taken from individually defined LO ROIs). Time courses for objects in the LVF (solid red line) show a larger response than those in the UVF (solid blue line), and scrambled versions of these objects also show a larger response in the LVF (dashed red line) than in the UVF (dashed blue line). Gray lines show LO responses to objects and scrambled counterparts presented at central fixation (these data were not included in our statistical analyses because they were used to define our ROI). The duration of each experimental block is shaded in gray. Horizontal brackets are shown above each set of time courses to indicate which time points were used in our statistical analyses. *C:* differences ($UVF_{objects} - UVF_{scrambled}$ and $LVF_{objects} - LVF_{scrambled}$) were computed from the data in *B* for all 3 stimulus locations (colors correspond to those used in *B*). Note that the differences between UVF and LVF time course data shown in *B* disappear when the response to scrambled objects is subtracted from that of objects.

from the UVF and LVF conditions were not used to define our LO ROI). When necessary, we also took into account anatomical cues, as described in various other studies (Sayres and Grill-Spector 2008). LO was always situated along the lateral extent of the occipital lobe, which is anatomically distinct from other object-selective regions in ventral visual cortex.

RESULTS

Object selectivity and position sensitivity in LO

We first compared BOLD responses to objects and scrambled objects in individually defined LO ROIs (see *ROI selection*). Note that the comparisons and supporting statistics reported here correspond to the UVF- and LVF-presented stimuli because data from the centrally presented stimuli were used to define our LO ROI.

For each individual (and each hemisphere, separately) we computed the mean BOLD response in LO from 6 to 14 s after the onset of the first stimulus. All statistical analyses were performed on BOLD responses within this time frame; we denote this with the horizontal bar in Figs. 2 and 4. We conducted two separate 2×2 repeated-measures ANOVAs on these data (1 ANOVA per hemisphere). Consistent with our expectations for LO, we found a highly significant main effect of stimulus type in the data for each hemisphere, with BOLD responses to objects being greater than those to scrambled objects [right hemisphere: $F(1,13) = 86.89$, $P < 0.0001$; left hemisphere: $F(1,13) = 64.69$, $P < 0.0001$]. We also found a highly significant main effect of stimulus location, with BOLD responses to LVF stimuli being greater than those to UVF stimuli [right hemisphere: $F(1,13) = 11.75$, $P < 0.05$; left hemisphere: $F(1,13) = 6.59$, $P < 0.05$]. We did not observe a significant interaction of our independent variables for either hemisphere (both $P > 0.05$). Because the pattern of results was identical for the two hemispheres, we averaged the data between the two hemispheres within each individual. The time courses for all conditions are shown in Fig. 2*B*.

We next investigated our primary research question. Does object selectivity vary as a function of stimulus location? We computed our measure of object selectivity as the difference between BOLD responses to objects and scrambled objects within either the UVF or LVF (i.e., $UVF_{objects} - UVF_{scrambled}$ and $LVF_{objects} - LVF_{scrambled}$). These data are shown in Fig. 2*C*. A paired-samples *t*-test failed to show any significant difference using this measure for UVF-presented stimuli (Fig. 2*C*, blue line) and LVF-presented stimuli (Fig. 2*C*, red line; $P = 0.75$). To summarize, although the overall magnitude of the BOLD response was higher for LVF stimuli than for UVF stimuli (Fig. 2*B*, both for objects and scrambled objects), this effect was not found for our measure of object selectivity (Fig. 2*C*).

Polar angle maps and maximal effects of stimulus location in LO

We obtained retinotopic maps using a cross-correlation analysis (Bandettini et al. 1993; Serences and Yantis 2007). 2-D cross-correlation maps for three representative individuals are shown in Fig. 3 using color-coded lag values (blue = UVF; red = LVF; green = 90°, i.e., 9 o'clock position, in the left visual field), where the lag of the maximum correlation denotes the angular position of the rotating wedge stimulus. The blue and red squares in Fig. 3 indicate the cortical locations of maximal effects of stimulus location in LO in *experiment 1*. For each individual, we contrasted responses to UVF and LVF stimuli (in each case, responses to objects and scrambled objects were combined; as such, these responses were not specific to either objects or scrambled objects). The blue and red squares in Fig. 3 indicate the cortical location of the most significant contiguous cluster of ≤10 voxels within each individually defined LO ROI for UVF and LVF

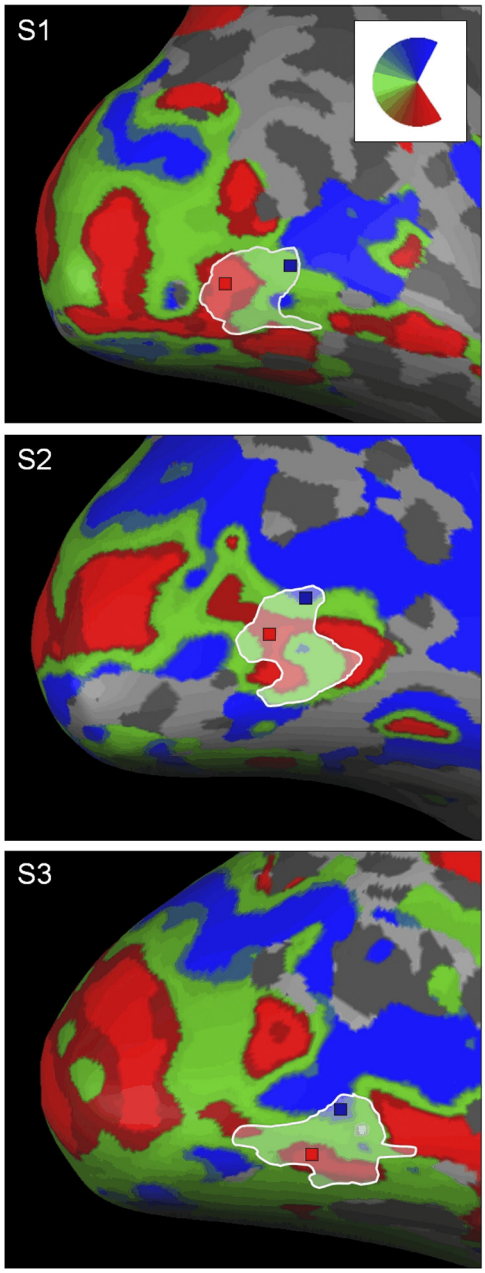

FIG. 3. Maximal sensitivity to stimulus location in *experiment 1* corresponded to the retinotopic maps obtained in *experiment 2*. The maximal location-specific responses in *experiment 1* (blue square = UVF stimuli and red square = LVF stimuli) are superimposed on corresponding polar angle maps (LVF = red; UVF = blue; contralateral visual field = green) obtained in *experiment 2* for 3 representative subjects. LO is indicated by the white outline).

stimuli, respectively. The locations of these peaks are superimposed on the retinotopic maps obtained in *experiment 2*.

In all subjects for whom we obtained retinotopic maps, we observed maximal location-specific responses (from *experiment 1*) that perfectly matched the subject's retinotopy data. That is, the locations of peak UVF (Fig. 3, blue squares) and LVF (Fig. 3, red squares) responses in *experiment 1* always predicted the polar angle preferences indicated by an individual's retinotopic map. In most subjects, the LVF (red square) responses were largely centered within LO, whereas the UVF (blue square) responses were situated most often toward the anterior edge of LO. A similar pattern was observed for the retinotopic maps, with the LVF map (Fig. 3, red) accounting for more of LO than the UVF map (Fig. 3, blue), which showed relatively little overlap with LO.

Cortical distribution of maximal position sensitivity and object selectivity

We conducted a final analysis to study the spatial distribution of our LO sub-ROIs (defined earlier) in Talairach space. For purposes of comparison, we also examined this in V4v, which is known to have distinct cortical representations of the two visual fields (we did not observe any significant object selectivity effects in V4v when we performed an ANOVA analogous to those reported earlier for LO).

Consistent with a previous finding by Large et al. (2008), we found that UVF representations in V4v were consistently more medial than LVF representations. This pattern is seen in the *top panels* of Fig. 4, which shows the x and y Talairach coordinates for the individual subjects (small blue/red squares) and group means (larger blue/red dots). The only significant difference in Talairach location across individuals was observed along the x dimension. This difference was highly significant ($P < 10^{-6}$ for each hemisphere) and reflects the high degree of intersubject consistency in medial-lateral relative peak locations for UVF and LVF stimuli, respectively. Unlike our results for V4v, we did not observe a significant medial-lateral UVF and LVF distinction in LO for either hemisphere ($P > 0.05$ for both hemispheres). This is evident in the overlapping blue/red dots in the *middle row* in Fig. 4.

Finally, we assessed whether object selectivity in the UVF and the LVF corresponded to different cortical subregions of LO. We performed separate object-scrambled contrasts for each location (UVF and LVF) to see whether different peaks could be identified for each within our LO ROI. The Talairach coordinates of these peaks are shown in the *bottom two panels* in Fig. 4 (LO*). As observed in our UVF-LVF comparison in LO (Fig. 4, *middle panels*), we again found overlapping group means for UVF and LVF peak locations (indicated by overlapping dots, similar to those observed in the *middle panels* of Fig. 4); these were not significantly different for either hemisphere ($P > 0.05$ for both hemispheres). However, unlike the peak locations for UVF and LVF stimulus locations shown in the *middle panels* of Fig. 4, the peak locations for the current comparison were more proximate for the majority of our subjects. As indicated by the blue/red squares (mostly connected by short lines) in the *bottom panels* of Fig. 4, most of the individuals had adjacent or overlapping peaks of activation.

Our failure to observe significantly disparate peaks of activation for our location-specific analysis (Fig. 4, *middle panels*) resulted from an inconsistency in the relative locations (i.e., directions of each along the x dimension) of UVF and LVF peaks. In contrast, in the LO* analysis (Fig. 4, *bottom panels*), there is both an inconsistency in these relative locations and also a general lack of cortical separation (which is indicated by the relatively short gray lines connecting the blue/red squares compared with those in the previous panels). We addressed this further by performing additional statistical analyses of the absolute cortical distances in 3-D Talairach space for the data reported in Fig. 4.

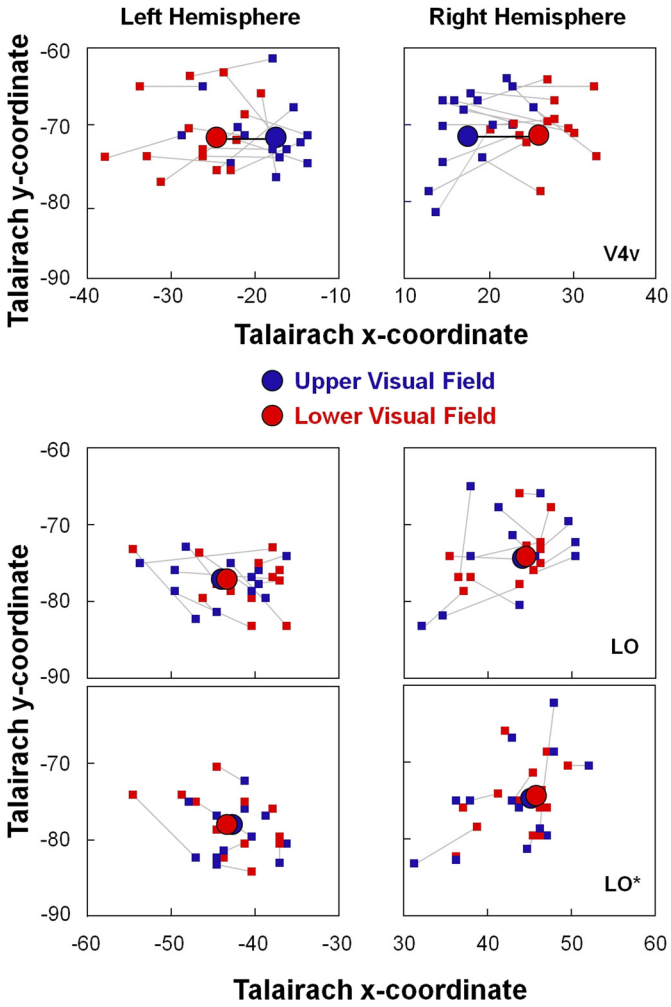

FIG. 4. We observed distinguishable cortical representations for UVF and LVF stimuli in V4 and LO (blue square = UVF and red square = LVF). These were consistent in relative location across individuals for V4 but not LO. Talairach coordinates for peak activation for UVF and LVF stimuli in *experiment 1*. Coordinates for individuals are also shown (connected by a line for each individual). Group mean peak coordinates for V4v (UVF = black dot; LVF = white dot). *Middle row* of panels shows coordinates for the same peak activations in LO. The *bottom panels* (LO*) report coordinates for separate UVF and LVF object-selectivity comparisons (i.e., $UVF_{objects} - UVF_{scrambled}$ and $LVF_{objects} - LVF_{scrambled}$).

Figure 5 shows the magnitudes of *x*, *y*, and *z* distances for UVF and LVF peak locations assessed in the previous three analyses. Unlike those corresponding to the group data reported in Fig. 4 (blue/red dots), the values in Fig. 5 were computed irrespective of the relative UVF-LVF positions in each dimension (i.e., the absolute value of the Talairach distance). As expected, these distances were largest in area V4v, along the *x* dimension, which differed significantly from those along the *y* and *z* dimensions (both $P < 0.05$). Peaks along the *y* and *z* dimensions did not differ ($P = 0.64$). Similarly, in LO, we also observed a significantly larger distance along the *x* dimension compared with the others (both $P < 0.05$) but no difference between *y* and *z* ($P = 0.41$). We observed the smallest cortical distances within subjects for the object selectivity comparison (LO*). We even failed to observe significant differences along the *x* dimension compared with *y* and *z* (right bars in Fig. 5). None of these values were significantly different from each other ($P > 0.05$ for all possible paired comparisons). In short, we did not observe a consistent medial-lateral separation of peak responses corresponding to the UVF and LVF in LO (Fig. 4), but we nevertheless observed consistent and significant separation along the *x* dimension compared with that in the *y* and *z* dimensions (Fig. 5). We did not, however, observe this in our object selectivity analysis (Figs. 4 and 5, LO*).

DISCUSSION

Our results suggest that neural activity in LO in response to objects is modulated by their position in the visual field. In agreement with the work of Sayres and Grill-Spector (2008) and others (Grill-Spector et al. 1999; Large et al. 2008; Niemeier et al. 2005), we observed greater activation for LVF objects compared with UVF objects. Crucially, we observed an equivalent effect of stimulus location for scrambled objects (Fig. 2*B*). Finally, we found that UVF and LVF representations in LO were spatially segregated in the cortex of individual subjects but, in contrast to V4v, did not exhibit consistent relative locations in Talairach space when averaged across subjects (Figs. 4 and 5). We found no evidence of cortical segregation for LO* coordinates, which we obtained using independent contrasts for UVF-presented stimuli ($UVF_{objects} - UVF_{scrambled}$) and LVF-presented stimuli ($LVF_{objects} - LVF_{scrambled}$).

Is LO sensitive to stimulus location?

Our experiments yielded mutually supportive results that suggest LO is sensitive to the location of a stimulus in the visual field. In *experiment 1,* we observed that LO responses to both objects and non-objects were modulated by stimulus position (Fig. 2*A*). We also found that the UVF and LVF sub-ROIs identified in LO using the stimuli from *experiment 1* agreed with the retinotopic maps obtained in *experiment 2* (Fig. 3). Our results corroborate recent work by Sayres and Grill-Spector (2008), who observed both a greater number of voxels preferring the LVF to the UVF in LO and greater mean

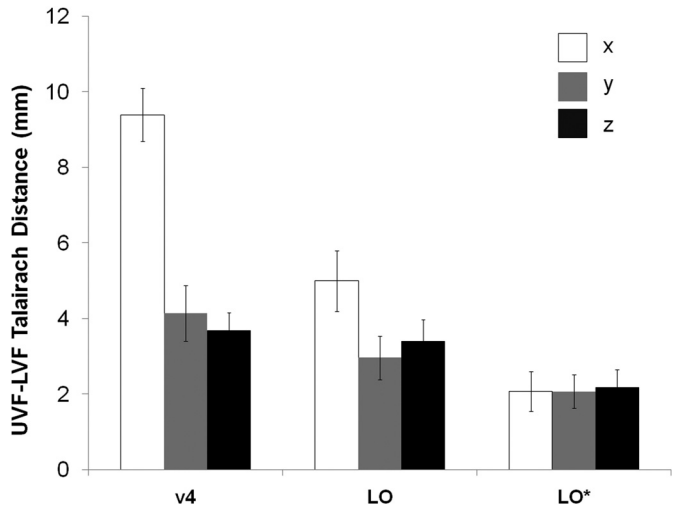

FIG. 5. Mean absolute values of the Talairach distances between UVF and LVF peaks in V4v and LO showed the greatest distances along the *x* Talairach dimension. This was not observed for LO* (i.e., $UVF_{objects} - UVF_{scrambled}$ and $LVF_{objects} - LVF_{scrambled}$). The distances reported here correspond to the mean lengths of the gray lines in Fig. 4.

responses to objects presented in the LVF than to those presented in the UVF for both objects and non-object stimuli. Our findings are consistent with a growing number of studies suggesting the representation of stimulus location information in LO (Carlson et al. 2009; Grill-Spector et al. 1998; Hemond et al. 2007; Large et al. 2008; Levy et al. 2001; McKyton and Zohary 2007; Niemeier et al. 2005; Schwarzlose et al. 2008; Tootell and Hadjikhani 2001; Tyler et al. 2005).

Equal degrees of object selectivity in LO

Of primary interest in our study was the prospective relationship between object selectivity (i.e., the magnitude of $BOLD_{objects} - BOLD_{scrambled}$) and the observed sensitivity to stimulus position (UVF or LVF) in LO. Two previous studies reported the representation of stimulus location information in LO (Sayres and Grill-Spector 2008; Schwarzlose et al. 2008). In these studies, LO was defined by its object-selective response. However, the reported position dependence of LO in these studies was derived solely from the BOLD response to objects and not from the object-selective response. In the study by Sayres and Grill-Spector (2008), although they purported in their title to relate object-selective responses to retinotopy, their method did not actually allow them to address this relation; the authors could only infer it because their object and non-object stimuli were not equated for position or size and were presented in different experiments and also because the fMRI results for their object stimuli were compared with a fixation baseline rather than to non-objects directly). Because we paired objects with their scrambled counterparts, we were able to make an important and novel observation: object-selectivity in LO does not vary with stimulus location. Our finding suggests that, even though the UVF is under-represented in LO relative to the LVF, LO nevertheless discriminates objects from non-objects equally well (in terms of BOLD response) in either location.

Cortical distribution of UVF and LVF representations

Sayres and Grill-Spector (2008) did not find any UVF object-preferring voxels in LO even though their retinotopy data showed UVF-preferring voxels. Our results were similar to those of Sayres and Grill-Spector in that UVF-preferring voxels in both of our experiments did not exhibit as much overlap with LO as the LVF-preferring voxels (Fig. 3). This suggests that, although the UVF may indeed be under-represented in LO (relative to the LVF), cortically distinct UVF and LVF representations in LO are equally object selective.

We also sought separable UVF and LVF representations in LO. In V4v, we observed a medial-lateral arrangement of UVF and LVF representations (Fig. 5), where the UVF representation was more medial than the LVF representation. This finding is in agreement with previous reports (Bartels and Zeki 1998; Large et al. 2008; McKeefry and Zeki 1997; Wade et al. 2002; Zeki 2001) and was highly consistent across our subjects. The corresponding representations in LO were distinguishable within individual subjects, but because there was a lack of consistent directionality along the *x*-axis between individual subjects, the consistent medial-lateral organization observed in V4v was not observed in LO (Fig. 5). This corroborates similar reports of intersubject inconsistency in the retinotopic organization of LO (Large et al. 2008; Larsson and Heeger 2006; Sayres and Grill-Spector 2008). Nevertheless, we did find strong evidence of cortical segregation of UVF and LVF representations in LO when we disregarded the relative positions of these representations. We are confident that our peaks accurately reflected locations of maximal sensitivity to stimulus location because the UVF and LVF peaks were always consistent with our observed retinotopic maps.

Finally, we tested whether we could identify distinguishable peaks of activation for maximum object selectivity at different locations within LO (Figs. 4 and 5, LO*). Because object selectivity is conventionally gauged by comparing responses to objects versus scrambled objects, we used this type of comparison to localize object-selective peaks of activation in LO. We identified cortical locations within LO that responded maximally to objects compared with scrambled objects, each presented in the same location (either the UVF or LVF). This analysis did not result in consistently distinguishable locations of peak cortical activity. Instead, we found that, for the majority of our participants, the resultant peaks of activation were highly overlapping. This is consistent with a similar analysis by Large et al. (2008), who reported overlapping peaks of activation to object animations presented at different locations in the visual field. In short, although we found evidence for distinct UVF and LVF representations in LO, the locations of these representations were not the same as those derived by making location-specific comparisons of object selectivity.

Conclusions

Our delineation of UVF- and LVF-specific sub-ROIs in LO and our observation of equal degrees of object selectivity for the two corresponding stimulus position points to at least two neural scales at which we might account for our results. At the finest scale, we might posit that the responses of individual LO neurons depend on conjoint stimulus category and location information. Given that LO seems to have distinct UVF and LVF representations, it is possible that position sensitivity is a fundamental organizing principle in LO and applies to all neurons therein. That is, not only are the response of these neurons modulated by position, the cortical locations of these neurons are spatially segregated according to position sensitivity in addition to object selectivity. A second coarser scale possibility is that LO contains two intermingled populations of neurons, both of which respond more strongly to objects than non-objects: one that is sensitive to stimulus position and another that is not. The combined responses of these two intermingled populations could, in principle, give rise to the pattern of results we observed. Additional studies are necessary to determine whether spatially distinct UVF- and LVF-preferring regions of LO are comprised of neurons that code for both objects and their locations conjointly or intermingled populations in which only some neurons are sensitive to stimulus position. The same caveat holds for the observation of position sensitivity in the responses of neurons within the fusiform face area (FFA) and other ventral visual areas by Schwarzlose et al. (2008). It may be that, as we observed for object selectivity in LO, face selectivity in FFA also does not vary with stimulus position.

In terms of object recognition, our finding that object selectivity is equal for neural subpopulations within LO with disparate position specificities implies that these two sets of

neurons can discriminate objects from non-object stimuli equally well in preferred and nonpreferred visual field locations. In this sense, object recognition performance is the same despite differences in the magnitude of the underlying neural response. Additionally, our finding that the LVF bias observed by Sayres and Grill-Spector (2008) applies equally to object and non-object stimuli may suggest that LVF advantages reported in a variety of perceptual tasks (Christman 1993; Levine and McAnany 2005; Rubin et al. 1996) and visual motor tasks (Danckert and Goodale 2001, 2005) originate from regions before LO, one of these being the greater proportion of ganglion cells in superior retina (Curcio and Allen 1990). Although our findings corroborate accumulating evidence in favor of retinal position effects throughout the occipito-temporal cortex (Carlson et al. 2009; Hansen et al. 2007; Hasson et al. 2003; Hemond et al. 2007; Large et al. 2008; Levy et al. 2001; McKyton and Zohary 2007; Niemeier et al. 2005; Sayres and Grill-Spector 2008; Schwarzlose et al. 2008), our findings further refine our understanding of the relation between retinotopic maps in LO and object selectivity.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

REFERENCES

Bandettini PA, Jesmanowicz A, Wong EC, Hyde JS. Processing strategies for time-course data sets in functional MRI of the human brain. *Magn Reson Med* 30: 161–173, 1993.

Bartels A, Zeki S. The theory of multistage integration in the visual brain. *Proc Royal Soc* 265: 2327–2332, 1998.

Carlson T, Hogendoorn H, Fonteijn H, Verstraten FA. Spatial coding and invariance in object-selective cortex. *Cortex* In press.

Christman SD. Local-global processing in the upper versus lower visual fields. *Bull Psychonomic Soc* 31: 275–278, 1993.

Curcio CA, Allen KA. Topography of ganglion cells in human retina. *J Comp Neurol* 300: 5–25, 1990.

Danckert J, Goodale MA. Superior performance for visually guided pointing in the lower visual field. *Exp Brain Res* 137: 303–308, 2001.

Danckert J, Goodale MA. Ups and downs in the visual control of action. In: *Taking Action: Cognitive Neuroscience Perspectives on Intentional Actions*, edited by Johnson-Frey SH. Cambridge, MA: MIT Press, 2004, p. 29–64.

Edelman S, Poggio T. Models of object recognition. *Curr Opin Neurobiol* 1: 270–273, 1991.

Grill-Spector K, Kushnir T, Edelman S, Avidan G, Itzchak Y, Malach R. Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* 24: 187–203, 1999.

Grill-Spector K, Kushnir T, Hendler T, Edelman S, Itzchak Y, Malach R. A sequence of object-processing stages revealed by fMRI in the human occipital lobe. *Hum Brain Mapp* 6: 316–328, 1998.

Grill-Spector K, Kushnir T, Hendler T, Malach R. The dynamics of object-selective activation correlate with recognition performance in humans. *Nat Neurosci* 3: 837–843, 2000.

Hansen KA, Kay KN, Gallant JL. Topographic organization in and near human visual area V4. *J Neurosci* 27: 11896–11911, 2007.

Hasson U, Harel M, Levy I, Malach R. Large-scale mirror-symmetry organization of human occipito-temporal object areas. *Neuron* 37: 1027–1041, 2003.

Hasson U, Levy I, Behrmann M, Hendler T, Malach R. Eccentricity bias as an organizing principle for human high-order object areas. *Neuron* 34: 479–490, 2002.

Hemond CC, Kanwisher NG, Op de Beeck HP. A preference for contralateral stimuli in human object- and face-selective cortex. *PLoS ONE* 2: e574, 2007.

Kourtzi Z, Kanwisher N. Cortical regions involved in perceiving object shape. *J Neurosci* 20: 3310–3318, 2000.

Kravitz DJ, Vinson LD, Baker CI. How position dependent is visual object recognition? *Trends Cogn Sci* 12: 114–122, 2008.

Large ME, Culham J, Kuchinad A, Aldcroft A, Vilis T. fMRI reveals greater within- than between-hemifield integration in the human lateral occipital cortex. *Eur J Neurosci* 27: 3299–3309, 2008.

Larsson J, Heeger DJ. Two retinotopic visual areas in human lateral occipital cortex. *J Neurosci* 26: 13128–13142, 2006.

Lerner Y, Hendler T, Ben-Bashat D, Harel M, Malach R. A hierarchical axis of object processing stages in the human visual cortex. *Cereb Cortex* 11: 287–297, 2001.

Levine MW, McAnany JJ. The relative capabilities of the upper and lower visual hemifields. *Vision Res* 45: 2820–2830, 2005.

Levy I, Hasson U, Avidan G, Hendler T, Malach R. Center-periphery organization of human object areas. *Nat Neurosci* 4: 533–539, 2001.

Logothetis NK, Sheinberg DL. Visual object recognition. *Annu Rev Neurosci* 19: 577–621, 1996.

Malach R, Levy I, Hasson U. The topography of high-order human object areas. *Trends Cogn Sci* 6: 176–184, 2002.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc Natl Acad Sci USA* 92: 8135–8139, 1995.

McKeefry DJ, Zeki S. The position and topography of the human colour centre as revealed by functional magnetic resonance imaging. *Brain* 120: 2229–2242, 1997.

McKyton A, Zohary E. Beyond retinotopic mapping: the spatial representation of objects in the human lateral occipital complex. *Cereb Cortex* 17: 1164–1172, 2007.

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.

Rubin N, Nakayama K, Shapley R. Enhanced perception of illusory contours in the lower versus upper visual hemifields. *Science NY* 271: 651–653, 1996.

Sayres R, Grill-Spector K. Relating retinotopic and object-selective responses in human lateral occipital cortex. *J Neurophysiol* 100: 249–267, 2008.

Schwarzlose RF, Swisher JD, Dang S, Kanwisher N. The distribution of category and location information across object-selective regions in human visual cortex. *Proc Natl Acad Sci USA* 105: 4447–4452, 2008.

Serences JT, Yantis S. Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cereb Cortex* 17: 284–293, 2007.

Talairach J, Tournoux P. *Co-planar Stereotaxic Atlas of the Human Brain : 3-Dimensional Proportional System: An Approach to Cerebral Imaging*. Stuttgart, New York: Thieme Medical Publishers, 1988.

Tanaka K. Inferotemporal cortex and object vision. *Annu Rev Neurosci* 19: 109–139, 1996.

Tootell RB, Hadjikhani N. Where is 'dorsal V4′ in human visual cortex? Retinotopic, topographic and functional evidence. *Cereb Cortex* 11: 298–311, 2001.

Tyler CW, Baseler HA, Kontsevich LL, Likova LT, Wade AR, Wandell BA. Predominantly extra-retinotopic cortical response to pattern symmetry. *Neuroimage* 24: 306–314, 2005.

Wade AR, Brewer AA, Rieger JW, Wandell BA. Functional measurements of human ventral occipital cortex: retinotopy and colour. *Philos Trans R Soc Lond* 357: 963–973, 2002.

Zeki S. Localization and globalization in conscious vision. *Annu Rev Neurosci* 24: 57–86, 2001.