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A contralateral preference in the lateral occipital area: sensory and attentional mechanisms.

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A Contralateral Preference in the Lateral Occipital Area: Sensory and Attentional Mechanisms

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Here we examined the level of the lateral occipital (LO) area within the processing stream of the ventral visual cortex. An important determinant of an area's level of processing is whether it codes visual elements on both sides of the visual field, as do higher visual areas, or prefers those in the contralateral visual field, as do early visual areas. The former would suggest that LO, on one side, combines bilateral visual elements into a whole, while the latter suggests that it codes only the parts of forms. We showed that LO has a relative preference for visual objects in the contralateral visual field. LO responses were influenced by attention. However, relative changes in LO activity caused by changes in object location were preserved even when attention was shifted away from the objects to moving random dot patterns on the opposite side. Our data offer a new view on LO as an intermediate, but not a high-level, visual area in which neurons are driven by visual input and spatial attention in a multiplicative fashion.

Keywords: attention, fMRI, motion, object perception, topography

Introduction

Among the 30 or so visual areas in the cortex (Felleman and Van Essen, 1991; Tanaka, 1996; Tootell *et al.*, 1996), the early ones, closer to the retina, show a spatial organization that is strongly retinotopic: these areas map the visual field in an orderly fashion so that separate parts of cortex represent distinct regions of the visual field (e.g. Sereno *et al.*, 1995). Areas farther away from the retina are less retinotopic, and in high-level areas each patch of cortex responds to visual stimuli from the right and left visual field so that the topographic organization is lost (e.g. Kanwisher *et al.*, 1997a). At the same time, the size of receptive fields, the portions of the visual field to which neurons respond, increases (e.g. Tanaka, 1996). The loss of spatial organization can be part of the process that makes object perception independent of the object's size and location on the retina. For instance, in the monkey, cells in the inferior temporal cortex are selectively activated by particular objects or object parts (for a review see Tanaka, 1996) and this activation is relatively independent of the size or location of the objects on the retina (Schwartz *et al.*, 1983). Thus, the degree of retinotopy can be used as a marker of an area's degree of positional invariance as part of the object processing within the ventral stream.

The human lateral occipital area LO, a subregion of the lateral occipital complex, represents an important stage in the visual processing of object form. It is located inferior and posterior to the motion area MT+ and responds more strongly to the images of objects than to scrambled versions of the images (Malach *et al.*, 1995; Kanwisher *et al.*, 1997b). Lesions in LO lead to visual form agnosia (James *et al.*, 2003). However, the level of LO in the hierarchy of the visual system is not clear. LO seems to occupy a high level within the visual system as it has been found to show very little retinotopy. LO, like areas of the fusiform gyrus, has a preference for the central field (Levy *et al.*, 2001), is activated by form regardless of the cue (motion, texture or luminance contrast) that defines the form (Grill-Spector *et al.*, 1998a) and has been reported to respond almost equally to stimuli in the ipsi- and contralateral halves of the visual field (Grill-Spector *et al.*, 1998b; Tootell and Hadjikhani, 2001).

Theoretically, then, it would be advantageous if LO were spatially organized in a similar way to the human equivalent of the motion area MT, the part of the medio-temporal complex MT+ that shows a contralateral preference (Dukelow *et al.*, 2001; Huk *et al.*, 2002). MT+ lies adjacent to LO, and the two areas cooperate in extracting form from motion (Yin *et al.*, 2002; Ferber *et al.*, 2003). This cooperation may benefit from similar visual field preferences because there is less need for inter-hemispheric communication, which is slower and requires more energy than intra-hemispheric. Therefore, the aim of this study was to test whether LO's topographic organization might have been underestimated in previous studies.

Materials and Methods

Subjects

Ten subjects participated in our experiments: five in experiment 1a, five in experiment 1b and seven in experiment 2. Our subjects were healthy, paid volunteers who gave their informed written consent. All procedures were approved by the Ethics Review Board of the University of Western Ontario.

MRI Setup

We used a Varian/Siemens 4.0 Tesla whole body system (Palo Alto, California/Erlangen, Germany) and optimized signal-to-noise ratios with a 15.5 × 11.5 cm quadrature radio frequency surface coil centered over the subject's occipital pole. Functional data were collected with a navigator echo corrected T_2*-weighted gradient echo-planar imaging pulse sequence [T_R = 1.0 s, 2 shots; T_E = 15.0 ms; FA = 40°; voxel size = 3 × 3 × 3 mm (1.5 × 1.5 × 1.5 mm in experiment 1b); FOV = 19.2 cm, 15 contiguous slices parallel to the calcarine sulcus]. Functional data were superimposed on high-resolution (0.75 × 0.75 × 1.5 mm) inversion-prepared 3-D T_1-weighted anatomical images of the brain collected immediately after the functional images using the same in-plane field of view (T_I = 800 ms; T_R = 9.6 ms; T_E = 5.2 ms). Subsequently the scans were aligned to an anatomic image obtained with a full head coil (T_I = 900 ms; T_R = 760 ms; T_E = 5.3 ms; voxel size = 1 × 1 × 1 mm; FOV = 25.6 cm; 160 slices). We analyzed the data using BrainVoyager 4.6 software (Maastricht, The Netherlands).

Localizers

LO localizer

Visual presentation was programmed using Macromedia Flash. To identify object-sensitive cortical areas, we presented intact and scrambled versions of the same black-and-white line outlines of animal shapes.

The drawings were selected from a commercial object library from which we also selected the stimuli for the second experiment. The images, superimposed onto a square grid and back-projected onto a screen and viewed in a mirror, subtended 6° of visual angle (i.e. foveal and mid-eccentric parts of the visual field, e.g. Malach *et al.*, 2002). Twelve images were presented in each epoch at 1 s intervals. There were 18 epochs in each experimental run with ten scrambled and eight unscrambled epochs. To control attention, subjects pressed a key whenever they saw the same image twice in a row.

MT+ localizer
To reveal regions of cortex activated by visual motion, we alternately presented moving and stationary versions of the same image: a texture of randomly oriented line segments in an area that covered the whole screen (70° horizontally and 30° vertically). In each moving epoch, the texture moved in cycles of 2 s; it either rotated clockwise–counterclockwise (30°/s), translated leftward–rightward or upward–downward (8.75°/s), or it contracted and expanded (1.5-fold/s) while subjects fixated a small central stationary red dot. Eight epochs of moving stimuli and ten stationary epochs were each viewed for 12 s.

Experiment 1
We measured the fMRI blood-oxygen level dependent (BOLD) signal evoked by a movie played in a wedge-shaped aperture (Fig. 1*B*). Subjects fixated a red bull's eye at the center of the screen. The wedge-shaped movie was displayed in one of four locations relative to the fixation point. In experiment 1a this was to the right, to the left, above or below fixation. In experiment 1b the wedges were displayed along the 45° diagonals: up-right, down-right, down-left and up-left. Each wedge covered a 45° sector, and its tip was displaced 1° from the central fixation spot. The movie showed sequential segments of a popular animated film. The sequencing and location of the movies were programmed within Macromedia Flash. The control condition presented the same fixation bull's eye in the center of a dark screen. The

movies in the four quadrants and the control condition were played in 16 s epochs. The order of the epochs for one complete scan was: control, up, right, down, left, control, left, down, right, up, control, down, left, up, right, control, right, up, left, down, control and control. Each scan was repeated either three or four times, each time with different segments of the film.

Experiment 2
We measured the BOLD signal produced when subjects viewed line drawings of objects displayed over a rotating disc-shaped pattern of dots. In the control condition subjects fixated a central point flanked by two discs of stationary dots (eccentricity 4.5°, diameter 7°). In the six experimental conditions the two discs rotated (independently of each other) at an angular speed of 25°/s and were superimposed with the stationary outlines of objects on one or both sides. The six conditions were: (i) attend to the object on the left or (ii) to the one on the right (called 1-object task, Fig. 1*C*); (iii) attend to the moving dots on the left while an object is displayed on the right; (iv) attend to the moving dots on the right while an object is displayed on the left (motion task, Fig. 1*D*); (v) objects are shown on both sides, but attend to the object on the right; and (vi) the same, but attend to the object on the left (2-objects task, Fig. 1*E*). Attention was directed right or left by an arrow-shaped fixation point and by asking the subject to press a key (i) whenever the attended object faced to the right (a new object was displayed every 2 s) or (ii) whenever the attended dot motion switched from clockwise to counterclockwise (this occurred at random intervals which averaged 2 s). Each condition was displayed for a 16 s epoch. Each of the conditions was repeated four times in a pseudorandom order during a single 8 min scan. Each scan was repeated three or four times.

Data Analysis
Using general linear model analysis with a square-wave function convolved with the hemodynamic response, voxels were identified as activated when their significance of signal change exceeded $P < 0.00012$
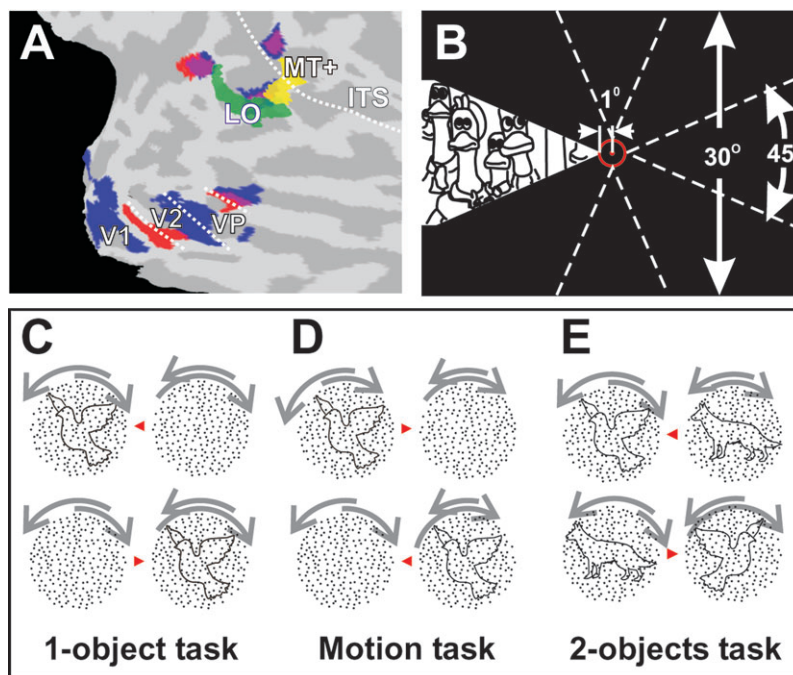

Figure 1. Experimental setup. (*A*) Areas LO and MT+ superimposed onto the right hemisphere of a virtually flattened brain. Activation produced by the object localizer (intact objects versus scrambled) defines area LO (shown in green). Activation produced by the motion localizer (motion vs. stationary) defines area MT+ (shown in yellow). Activation produced by the animated movie within a wedge-shaped aperture shown either to the left (blue) or above (red) of fixation can be used to define the borders of areas V1, V2 and VP in the lower right occipital cortex. ITS: inferior temporal sulcus. (*B*) In experiment 1a subjects watched scenes from an animated movie in a wedge-shaped aperture either left, right, above or below fixation. (*C–E*) Examples of stimuli used in experiment 2. Outlines of animal shapes and rotating random dot patterns were presented in the left and/or right visual hemifield. (*C*) In the 1-object task subjects attended to single outlines of animal shapes on the left (top row), or on the right (bottom row) while rotating random dot patterns appeared on both sides. (*D*) The motion task presented the same stimuli but subjects attended to the moving dots located opposite to the object (i.e. the dots on the right in the top row and on the left in the bottom row). (*E*) In the 2-object task objects and motion appeared on both sides. Subjects attended to the object on the left (top row) or on the right (bottom row).

and when they lay adjacent to six or more similarly identified voxels. LO was identified as the object-sensitive area (as found with the object localizer see above) immediately behind and below MT+ (Malach *et al.*, 1995). MT+ was defined as the motion-sensitive area (as marked by the motion localizer) at the junction of the inferior temporal and lateral occipital sulci (Watson *et al.*, 1993; Tootell *et al.*, 1995). Within these areas we located the geometric centers of activation and defined cubic regions of interest (ROIs, 10 × 10 × 10 mm in all experiments) and included all significantly activated voxels within these regions.

We then compared the activations in the LO and MT+ ROIs that were produced during the different epochs of experiments 1 and 2. We converted the data to percent signal change relative to the control periods and averaged activation within the last 10 s of each epoch to exclude delayed BOLD activity from the preceding epoch. We then normalized the data for each hemisphere separately, dividing the percent signal changes by the total average signal changes observed during the 'standard condition' (i.e. the contralateral wedges in experiment 1a, the lower contralateral wedges in experiment 1b and contralateral objects for the 1-object task of experiment 2).

For experiment 1a we calculated a multivariate 4 × 2 × 4 repeated-measures analysis of variance (ANOVA) with the factors Visual Field, Hemisphere and Epoch (i.e. four repeats for each condition within the averaged experimental run). Six 2 × 2 × 4 ANOVAs explored the significant effect of Visual field together with Holm's criterion to evaluate the *F*-tests. Another ANOVA compared effects of ipsilateral visual field stimulation in LO and MT+ (factors: Area, Hemisphere and Epoch). Furthermore, we looked for time-hemisphere interactions possibly caused by eye movements due to fatigue. To do this, we split the data into a first and a second half and performed a 4 × 2 × 2 ANOVA (factors: Area, Hemisphere and Half of Experiment) and, more specifically, two 2 × 2 ANOVAs (factors: Hemisphere and Half of Experiment), one for left and one for right visual field stimulation. For experiment 1b a 4 × 2 × 4 ANOVA for LO was performed (factors: Visual Field, Hemisphere and Epoch). It was followed by six 2 × 2 × 4 ANOVAs to further study the significant effect of Visual Field.

For experiment 2 we first calculated a general multivariate 3 × 2 × 2 × 4 ANOVA of all three tasks (factors: Task, Object Location, Hemisphere and Epoch). To analyze the significant effects (Task, Object Location and the Task × Object Location interaction) we conducted a 2 × 2 × 2 × 4 ANOVA in which we compared the 1-object task with the motion task. Additional 2 × 2 × 4 ANOVAs tested the influence of Object Location in these tasks separately. Another 2 × 2 × 4 ANOVA (factors: Location of Attentional Focus, Hemisphere and Epoch) examined the 2-objects task.

Results

Experiment 1: Visual Field Preferences

In experiment 1a subjects watched scenes from an animated movie through a wedge-shaped aperture in the left, right, upper or lower part of the visual field (Fig. 1*B*) while we measured the blood-oxygen level dependent (BOLD) signal within LO as defined by our localizer (Fig. 1*A*). The Talairach coordinates of LO (in mm ± SD) were −38 ± 4, −73 ± 7, −5 ± 2 for the left hemisphere and 45 ± 6, −71 ± 4 and −5 ± 5 for the right hemisphere. These coordinates are consistent with LO coordinates reported previously (e.g. Malach *et al.*, 1995; Grill-Spector *et al.*, 1998a).

Figure 2*A* shows the normalized BOLD signal changes in LO (see 'Data Analysis') for our five subjects as well as group averages. In a three-way ANOVA including all conditions (for details see Materials and Methods) we found activity in LO to vary with the location of the wedge-shaped aperture [Visual Field: $F(3,2) = 58.74$, $P = 0.0171$]. The response was nearly four times stronger when the aperture appeared contralateral rather than ipsilateral [$F(1,4) = 51.13$, $P = 0.002$]. Upper and lower field presentations elicited intermediate responses with some advantage to the lower field [$F(1,4) = 13.49$, $P = 0.021$]. No other effects were observed. The results were very similar in all
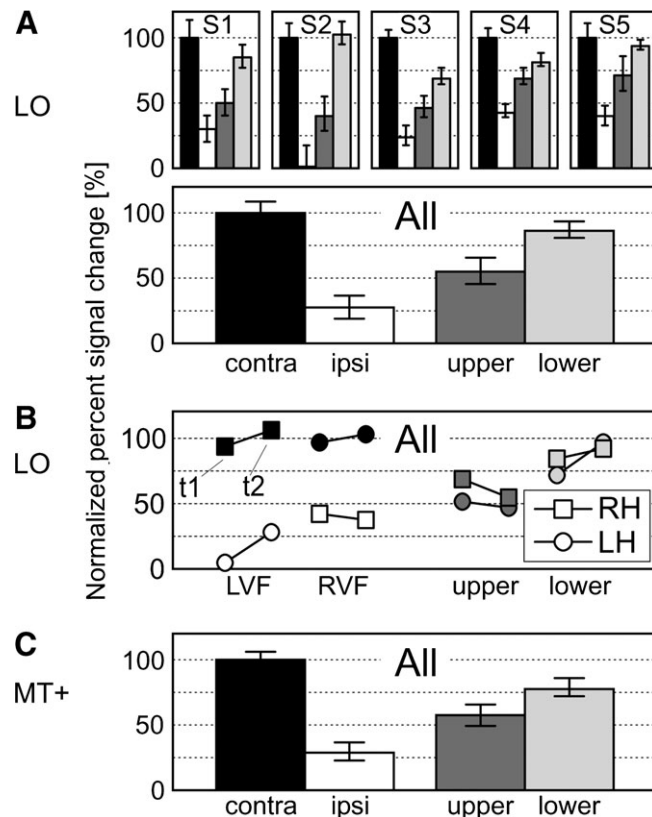

Figure 2. Normalized percent signal changes from experiment 1a. (*A*) Data for five subjects (averaged across epochs and hemispheres) and the group averages for LO. BOLD response was recorded for contra- and ipsilateral, upper or lower visual field stimulation. Error bars represent standard errors (subject data) or averaged standard errors (group data). (*B*) Group averages for LO separately for the first and second half of the experiment (t1 and t2) and hemispheres (RH, right hemisphere; LH, left hemisphere). Contra- and ipsilateral data are sorted by the absolute visual field location of the aperture: LVF, left visual field; RVF, right visual field. (*C*) Average data for MT+. Same conventions as in (*A*), lower panel.

subjects, showing that LO activity depends on the region of the visual field in which objects are presented.

This contralateral preference did not decay over time as would be expected if subjects had gotten tired and started looking directly at the movies. To check for this, we compared LO activity from the first and the second half of the experimental runs (Fig. 2*B*). We found no significant effect or interaction of time ($Ps \geq 0.095$) across the four visual field locations. For a separate analysis of left visual field stimulation there was only a main effect of time [$F(1,4) = 14.06$, $P = 0.020$], hence no evidence for reduced contralateral preference. The right visual field stimulation data even showed a (non-significant) trend in the opposite direction, that is, the preference rather increased (cf. Fig. 2*B*).

The contralateral visual field preference in LO was no less-pronounced than in the neighboring visual motion region MT+. We sampled a subset of voxels in MT+ that significantly preferred contralateral presentation of the movie, presumably corresponding to MT (Dukelow *et al.*, 2001; Huk *et al.*, 2002). Nevertheless, the average BOLD responses for the four visual field sectors were quite similar to those in LO (Fig. 2*C*), and an ANOVA testing the ratio of ipsilateral to contralateral activity showed no significant differences between LO and MT+ [$F(1,4) = 0.28$, $P = 0.625$].
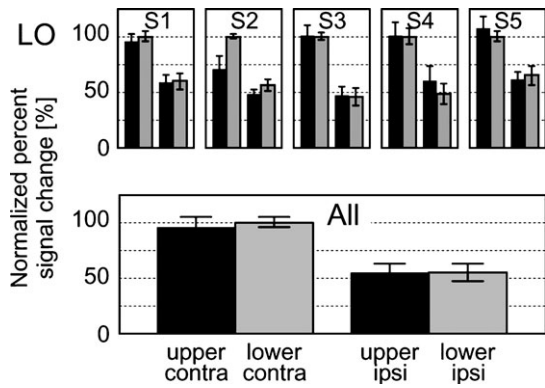
Figure 3. Normalized percent signal changes from experiment 1b. Data for five subjects (averaged across epochs and hemispheres) and the group averages for LO. BOLD response was recorded for upper and contralateral, lower and contralateral, upper and ipsilateral or lower and ipsilateral visual field stimulation. Error bars represent standard errors (subject data) or averaged standard errors (group data).

To confirm the contralateral preference observed in LO, in experiment 1b we repeated the experimental protocol with rotated apertures, now appearing along the 45° diagonals: up-right, down-right, down-left, and up-left (see Fig. 3). As before, we observed an overall influence of wedge location on LO activity as the only significant effect [Visual Field: $F(3,2) = 52.41$, $P = 0.0188$]. When we further explored the effect with ANOVAs comparing individual wedge locations (see Materials and Methods), both contralateral wedge locations (upper and lower visual field) yielded stronger responses than both ipsilateral ones [for all four analyses, $F(1,4) \geq 30.34$, $P \geq 0.0053$]. This pattern became obvious in all our subjects (Fig. 3). However, the contralateral preference was less marked than in experiment 1a and there was no significant difference between upper and lower visual field [$F(1,4) \leq 0.66$, $P \geq 0.46$], presumably because in experiment 1b the wedges lay closer to the meridians than the respective wedges in experiment 1a. That is, they lay closer to the vertical meridian than the previous contralateral and ipsilateral wedges and closer to the horizontal meridian than the previous upper and lower wedges.

Experiment 2: Attention and Contralateral Preference

The first objective of the second experiment was to corroborate the observation of experiment 1 that LO exhibits a contralateral bias, but by using a different experimental paradigm. Furthermore, it is possible that this contralateral preference is simply an artifact of attention. Therefore, the main objective of the second experiment was to study whether the contralateral preference merely reflects a spatially sensitive focus of attention that drives the BOLD signal regardless of whether a visual form is present in the left or the right visual half field. We addressed this question with three tasks (Fig. 1C–E). The resulting BOLD signal changes are given in Figure 4A as individual subject data as well as averages across subjects.

A very similar pattern was found in all seven subjects. In particular, the first two bars represent LO activity during the 1-object task, when the subjects attended to objects appearing exclusively on one side of the display. As in experiment 1, LO responded more strongly to contralateral than to ipsilateral

objects. More importantly, it did so even in the motion task, when subjects attended to the moving dots on the opposite side from the object.
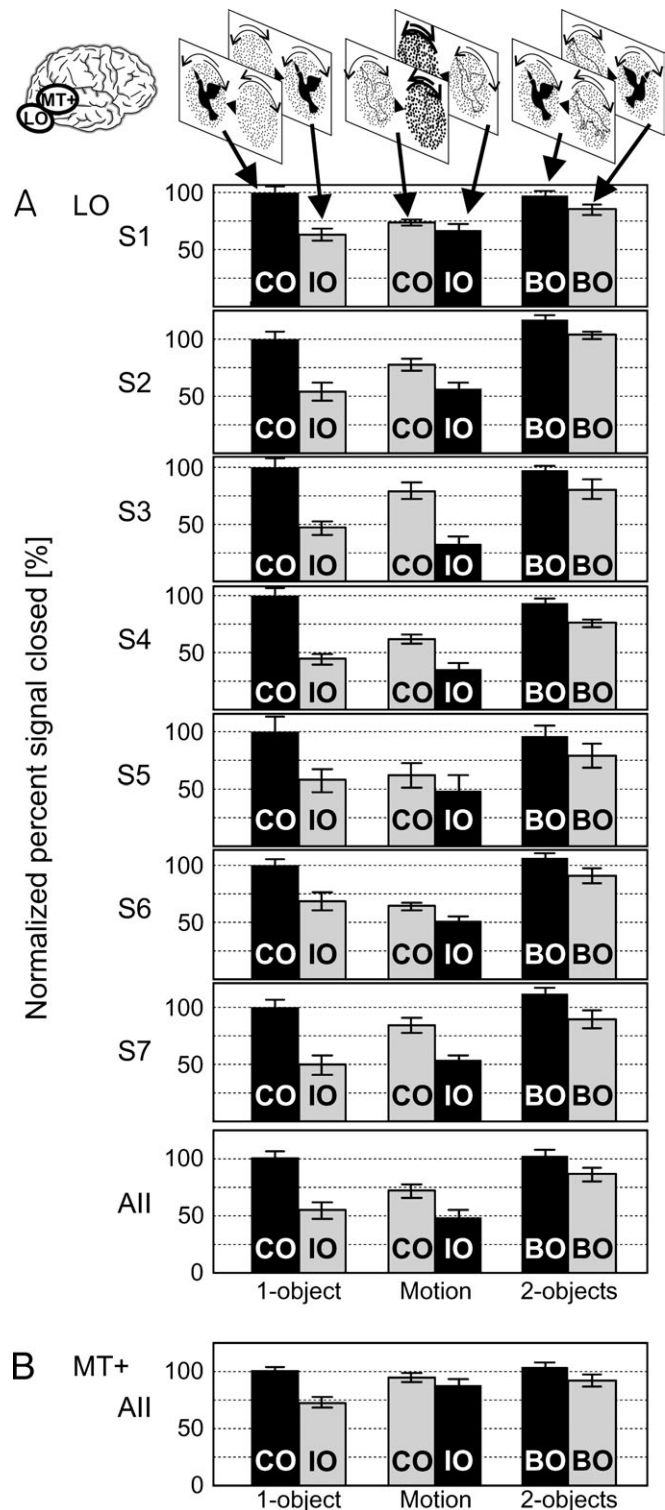

Figure 4. Normalized percent signal changes for experiment 2. (A) Group averages for LO. (B) Group averages for MT+. At the top of panel A, examples of the six conditions are shown from the perspective of the right hemisphere (actual data are collapsed across hemispheres). 1-object task, motion task, 2-objects task. CO: object presented contralaterally, IO: object presented ipsilaterally, BO: objects presented bilaterally. Black bars indicate that the side contralateral to the respective hemisphere was attended; gray bars indicate that the ipsilateral side was attended. Error bars represent averaged standard errors.

Consistent with this result, we found a significant influence of Object Location when testing effects across the 1-object task and the motion task [$F(1,6) = 73.40$, $P < 0.0005$] as well as in the separate tests for the 1-object task [$F(1,6) = 194.06$, $P < 0.0005$] and the motion task [$F(1,6) = 19.23$, $P = 0.005$]. This suggests that, no matter whether the subjects attended to the object or to the opposite side, LO responded more strongly when objects appeared in the contralateral visual field.

MT+ demonstrated a similar asymmetry during the 1-object task [$F(1,6) = 103.62$, $P < 0.0005$, Fig. 4B]. Most likely, the asymmetry was caused by attention and the stationary flashing objects, as MT+ responds to flicker (Tootell *et al.*, 1995). Indeed, even in the motion task MT+ responded strongly when the object appeared on the contralateral side, though subjects attended the rotating dots on the ipsilateral side. Because ipsilateral and contralateral MT+ did not differ significantly [$F(1,6) = 2.51$, $P = 0.164$], the asymmetrical activity in LO, in this condition, cannot be 'spillover' from the retinotopic MT.

However, LO was influenced by attention. It showed a significantly stronger BOLD signal in the 1-object task, when subjects attended to an object, than in the motion task, when they attended to the motion on the opposite side [factor Task: $F(1,6) = 31.12$, $P = 0.001$]. This cannot simply be due to a smaller cognitive effort in the motion task because MT+ showed the opposite pattern: more activity in the motion task [$F(1,6) = 9.35$, $P = 0.022$]. Further, in the 2-objects task, where objects were presented in both visual fields, activity in LO was influenced by the spatial focus of attention. LO responded more strongly when subjects attended to the contralateral object [$F(1,6) = 171.84$, $P < 0.0005$].

Do spatial attention and object location influence LO activity independently, or do they interact? Interestingly, the four-way ANOVA comparing the 1-object and motion tasks revealed a significant interaction between the factors Task and Object Location [$F(2,5) = 53.12$, $P < 0.0005$]. That is, switching from the contralateral object to the ipsilateral motion strongly decreased LO activity for contralateral objects by >25% [$F(1,6) = 68.89$, $P < 0.0005$]. But there was no significant decrease for ipsilateral objects [$F(1,6) = 2.44$, $P = 0.169$]. One interpretation is that object location and spatial attention 'truly' interact in a non-additive, probably multiplicative, fashion. Thus, attention would activate LO only if it is directed to an object on the contralateral side, but it would have a small effect when there is no contralateral object to focus on. If so, subjects with a relatively strong contralateral preference in LO should show this strong preference when attending to motion as well as when attending to the objects (Fig. 5A, left panel), and likewise subjects with a rather weak contralateral LO preference should have a weak contralateral preference when attending to either motion or the objects (Fig. 5A, right panel). Indeed, this is what we found. We calculated LO responses to ipsilateral object positions as a ratio (expressed in percentage) of those to contralateral objects. That is, we divided percent signal changes due to ipsilateral objects by those due to contralateral objects for each task separately (×100). The ratios for the 1-object task and the motion task were highly correlated across subjects ($r = 0.832$, $P = 0.02$, Fig. 5B; subtracting yields a similar correlation: $r = 0.809$, $P = 0.028$). This shows that the influence of object location was preserved across the two tasks, suggesting that the observed strong influences of attention largely worked in an interactive, e.g. multiplicative, way. In contrast, an independent (additive) effect of attention, if at all, must have been small because a large independent source of variability caused by attention in addition to that due to object
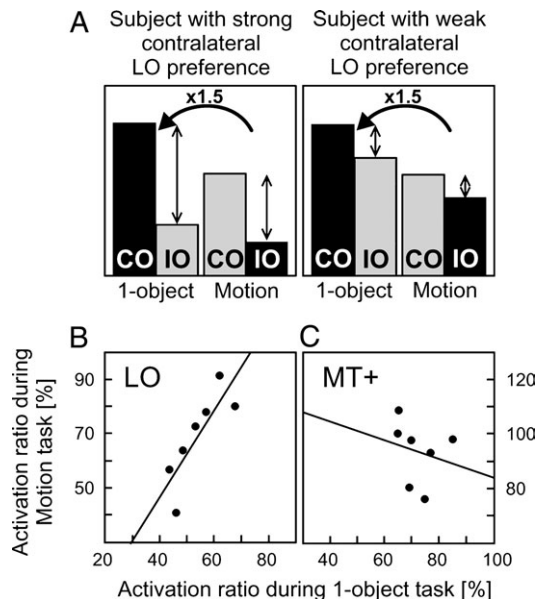

Figure 5. Differences of BOLD signal elicited by contralateral versus ipsilateral object position in experiment 2. (*A*) BOLD responses in two hypothetical subjects. A multiplicative influence of attention (here, ×1.5) would preserve the contralateral preference in LO so that subjects demonstrating either strong or weak contralateral preference in LO would do so in both the 1-object task and in the motion task. (*B*, *C*) Ratios of activation elicited by ipsilateral versus contralateral object position in experiment 2. Plotted are the data from seven subjects for the motion task as a function of the data for the 1-object task for LO (*B*) and for MT+ (*C*).

location would have wiped out the correlation. MT+ showed no comparable correlation ($r = -0.218$, $P = 0.639$, Fig. 5C; for absolute differences: $r = -0.198$, $P = 0.671$).

Discussion

Using fMRI, we have shown that the human visual-object area LO clearly preferred objects in the contralateral over those in the ipsilateral visual field. Further, we found some evidence that objects in the lower visual field elicited stronger responses than ones in the upper field; this finding is consistent with previous reports on LO (Grill-Spector *et al.*, 1999) and may reflect the visual system's superior performance in the lower visual field (Rubin *et al.*, 1996).

Within the contralateral field we found no evidence for topography as reported for early visual areas (Sereno *et al.*, 1995; Tootell *et al.*, 1996; Huk *et al.*, 2002), but LO degree of contralateral preference was similar to that in MT+. Both areas cooperate in tasks such as structure-from-motion (Yin *et al.*, 2002; Ferber *et al.*, 2003), and their cooperation may benefit from similar visual field representations.

Our data differ from a previous study that found only weak contralateral specialization in LO (Grill-Spector *et al.*, 1998b). One reason for the difference may be that Grill-Spector and colleagues used stimuli that covered visual half-fields including the fovea while our stimuli were displaced 1° from the center. It is possible that LO has a bilateral representation of the fovea and that visual field differences show up only for stimuli presented outside the fovea. Also, Grill-Spector and colleagues' stimuli bordered the vertical meridian whereas our stimuli lay farther apart. Indeed, experiment 1a and 1b together suggest that LO's contralateral preference increases with distance from the vertical meridian. Another difference may be that Grill-Spector

and colleagues' subjects viewed objects passively while performing a non-object-specific task, attending to and naming the colors of the central fixation cross. This is consistent with our finding in experiment 2, where in the non-object-specific task (i.e. the motion task) LO's preference for contralateral objects was reduced relative to the object-specific task (i.e. the 1-object task). Other studies presented no objects in the classical sense (e.g. Tootell and Hadjikhani, 2001).

Therefore, LO activation seems not only to depend on the sensory properties of the neurons in LO, but also on attention. Attention may have a non-spatial, task-related (object- versus motion-related) influence; a recent study found LO activity to drop when subjects switched from object perception to another task (Avidan *et al.*, 2003), and our data are consistent with this. More importantly, however, Avidan and colleagues found LO to be only slightly influenced by spatial attention; that is, the size of the attentional focus did not substantially matter (but see Seiffert *et al.*, 2003; Somers *et al.*, 1999; note, though, that the latter results may be influenced by changes in task-related attention). Our data suggest that it is the location of the focus of attention that influences LO activity. Attending to objects in the contralateral visual field activated LO ~19% more than attending to ipsilateral objects; thus, spatial attention has a substantial effect on lateralization in LO.

Is it possible that spatial attention is the only cause of LO lateralization? Though the motion task required a distribution of attention different from that of the 1-object task, detecting the motion changes may have been too easy to shift attention completely away from the objects to the opposite side, also producing a contralateral advantage of LO activity, as in the 1-object task. However, we found that across subjects the ipsilateral/contralateral difference in the 1-object task highly correlated with the difference in the motion task (Fig. 4A). The two tasks shared the same visual stimuli, so the correlation is strong evidence that LO's contralateral preference is based on neurons tuned to objects or object features in the contralateral visual field, regardless of the task.

Taken together, our data suggest that the object area LO retains a pronounced specialization for the contralateral visual field, in contrast to high-level visual areas with bilateral visual field representations (Tanaka, 1996; Kanwisher *et al.*, 1997a). This contralateral preference was amplified by attention. Together with the correlation in Figure 5*B*, our findings are consistent with the following view of attentional influences in LO: attention contributes to activity in a non-additive, perhaps roughly multiplicative, way — it accentuates neural responses when an object is present in a location for which the neurons are tuned but has little effect when there is no object. In this view, subjects in whom a large proportion of neurons in LO prefer visual objects on the contralateral side will also show strong effects of selective spatial attention, in keeping with Figure 5. Our data support the idea that a non-additive influence of attention enhances signal-to-noise ratios necessary to perceive stimuli embedded in our visually complex surroundings and to gate the information flow through the distributed processes of the human visual system (e.g. Treisman and Gelade, 1980; Desimone and Duncan, 1995; Kastner *et al.*, 1998).

Notes

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