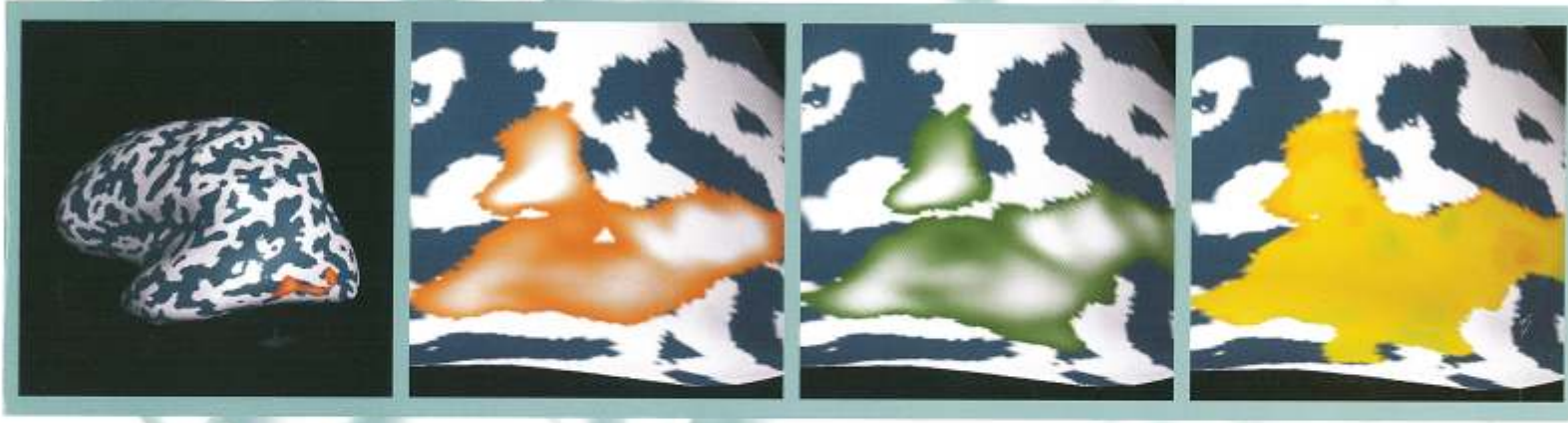
ISSN 0953-816X
http://www.blackwellpublishing.com/ejn

EJN

Volume 27 • Number 12 • June 2008



European Journal of Neuroscience

Cover Illustrations

fMRI of activation in the lateral occipital cortex (LO) of a representative subject. Activation peaks are represented by increased brightness. The LO is an object-selective region and was defined by contrasting intact vs. scrambled objects (far left panel). The other three panels show activation when the subject was asked to watch movies in the upper (UVF) or lower (LVF) visual fields: UVF vs. blank fixation control (left); LVF vs. blank fixation control (right) and UVF vs. LVF (far right). Note that the UVF and LVF peaks lie in the same location within the LO. For details, see the paper of M.-E. Large *et al.* (pp. 3299–3309).

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EJN
European Journal of Neuroscience

European Journal of Neuroscience, Vol. 27, pp. 3299–3309, 2008 doi:10.1111/j.1460-9568.2008.06270.x

fMRI reveals greater within- than between-hemifield integration in the human lateral occipital cortex

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Keywords: contralateral preference, functional imaging, humans, lateral occipital region, lower visual field, upper visual field

Abstract

Early visual areas within each hemisphere (V1, V2, V3/VP, V4v) contain distinct representations of the upper and lower quadrants of the contralateral hemifield. As receptive field size increases, the retinotopy in higher-tier visual areas becomes progressively less distinct. Using functional magnetic resonance imaging (fMRI) to map the visual fields, we found that an intermediate level visual area, the lateral occipital region (LO), contains retinotopic maps with a contralateral bias, but with a combined representation of the upper and lower visual field. Moreover, we used the technique of fMRI adaptation to determine whether neurons in LO code for both the upper and lower contralateral quadrants. We found that even when visual stimulus locations are equivalent across comparisons, the LO was more sensitive to location changes that crossed hemifields than location changes within a hemifield. These results suggested that within high-tier visual areas the increasing integration of visual field information is a two-stage process. The upper and lower visual representations are combined first, in LO, then the left and right representations. Furthermore, these results provided evidence for a neural mechanism to explain behavioral findings of greater integration within than between hemifields.

Introduction

Using visual field topography it is possible to delineate the spatial organization of the visual processing stream. Indeed, the functional organization of the early visual areas V1, V2 and V3/VP are fairly well established, and can be mapped using vertical and horizontal meridia (Fox *et al.*, 1987; Schneider *et al.*, 1993; Sereno *et al.*, 1995; DeYoe *et al.*, 1996; Dougherty *et al.*, 2003). Less well understood is the spatial organization of subsequent cortical regions in the visual hierarchy, such as the lateral occipital complex (LOC; Grill-Spector & Malach, 2004; Niemeier *et al.*, 2005; Wandell *et al.*, 2005), which are known to play an important role in object recognition (Malach *et al.*, 1995; Grill-Spector *et al.*, 1998). In a series of retinotopic mapping and functional magnetic resonance imaging (fMRI) adaptation experiments we explored the topography of the LOC to determine its role in generating holistic object representations, with particular emphasis on establishing at what point in the ventral cortical hierarchy, upper (UVF) and lower visual field (LVF) information is integrated.

It has been reported that LOC is only weakly retinotopic or non-retinotopic (Grill-Spector *et al.*, 1998; Tootell *et al.*, 1998; Tootell & Hadjikhani, 2001); however, more recent neuroimaging studies (Niemeier *et al.*, 2005; McKyton & Zohary, 2007; Hemond *et al.*, 2007) show a contralateral preference in lateral occipital region (LO)/LOC, suggesting some preserved topography in this region. However, these studies only examined left/right visual field differences, not UVF/LVF differences. Interestingly, Larsson & Heeger (2006) reported two visual field maps, named LO1 and LO2, localized to the lateral occipital region with distinct contralateral and UVF and LVF representations. The region LO2 was also activated preferentially for intact objects compared with scrambled objects, and may correspond to the dorsal caudal region referred to as LO in the literature (Grill-Spector *et al.*, 2000; Large *et al.*, 2005). Because more recent functional imaging studies have shown functional differences between subdivisions of LOC, we also confined our investigation to the dorsal caudal region called LO (Grill-Spector *et al.*, 1999, 2000; Kourtzi & Huberle, 2005; Large *et al.*, 2007).

Using the retinotopic mapping methods described in Niemeier *et al.* (2005) with standard-resolution ($3 \times 3 \times 5$ mm) and high-resolution ($1.5 \times 1.5 \times 1.5$ mm) fMRI designs, the first part of our study examined the representation of UVF and LVF in LO. We followed up with a high-resolution mapping experiment, as differences in the representation of UVF and LVF could be smeared with larger voxels sizes. If neurons in LO integrate information from UVF and LVF we would expect to see overlapping peaks of activation to UVF and LVF stimulation for both the high-resolution and standard-resolution mapping experiments. The second part of the study used an fMRI adaptation technique to determine whether neurons in LO code for both the upper and lower portions of the contralateral hemifield. We expected that if neurons in LO integrated information from UVF and LVF we would see a reduced blood-oxygen level dependent (BOLD) signal when the same stimulus was presented in different positions within a hemifield (i.e. vertical translations) compared with when the same stimulus was presented in different positions between hemifields (i.e. horizontal translations).

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Received 10 September 2007, revised 27 March 2008, accepted 17 April 2008

Materials and methods

Subjects

Eight healthy volunteers participated in the standard-resolution retinotopic mapping experiment (four male, four female); 11 volunteers participated in the high-resolution retinotopic mapping experiment (six male, five female). Thirteen volunteers participated in the translations across quadrants experiment (seven male, six female). All subjects gave written consent, and all procedures were approved by the University of Western Ontario Ethics Review Board, and in accordance with their guidelines.

fMRI

All three experiments were performed in a 4.0-Tesla Varian-Siemens (Erlangen, Germany) whole-body imaging system. In the standard-resolution retinotopic mapping experiment data were collected using a navigator echo-corrected T2*-weighted interleaved, two-segment, optimized spiral imaging sequence. A 15.5 × 11.5 cm quadrature radio frequency surface coil placed at the occipital pole was used to improve the signal-to-noise ratio. The parameters for the functional data were FOV = 19.2 × 19.2 cm; in-plane pixel size = 3 × 3 mm; TE = 15 ms; TR = 1 s (two shots), volume acquisition time = 2 s; FA = 60°; 17 coronal slices, slice thickness = 5 mm. The functional data were aligned to high-resolution inversion-prepared 3D T1*-weighted anatomical images with the following parameters: 96 slices; TE = 3 ms; TR = 50 ms; TI = 1300 ms; in-plane pixel size = 0.75 × 0.75 mm; slice thickness = 1.25 mm.

In the high-resolution retinotopic mapping experiment, data were collected using a navigator echo-corrected T2*-weighted segmented gradient echo planar pulse sequence (EPI) with the same surface coil as above. Functional data were collected using a volume acquisition time of 4 s (TR = 1 s, 4 shots; TE = 15.0 ms; FA = 40°; 1.5 × 1.5 × 1.5 mm for retinotopy; FOV = 19.2 cm, 11 contiguous slices parallel to the calcarine sulcus) and were aligned to high-resolution inversion-prepared 3D T1*-weighted anatomical images of the brain collected immediately after the functional images using the same in-plane field of view. The parameters for the EPI sequence anatomicals were 160 slices; TE = 5.2 ms; TR = 9.6 ms; TI = 800 ms; in-plane pixel size = 0.75 × 0.75 mm; slice thickness = 1.5 mm.

In the translation across quadrants experiment, data were collected using a navigator echo-corrected T2*-weighted interleaved, two-segment, optimized spiral imaging sequence with the same surface coil as above. The parameters for the functional data were: FOV = 19.2 × 19.2 cm; in-plane pixel size = 3 × 3 mm; TE = 15 ms; TR = 0. 75 s (two shots); volume acquisition time = 1.5 s; FA = 60°; 12 coronal slices, slice thickness = 5 mm. The functional data were aligned to high-resolution inversion-prepared 3D T1*-weighted anatomical images with the following parameters: 128 slices; TE = 3 ms; TR = 50 ms; TI = 1300 ms; in-plane pixel size = 0.8 × 0.8 mm; slice thickness = 1.25 mm.

The parameters for the object localizer scans performed for the retinotopic mapping experiments were: FOV = 19.2 × 19.2 cm; in-plane pixel size = 3 × 3 mm; TE = 15 ms; volume acquisition time = 2 s; FA = 40 °; 15 contiguous slices parallel to the calcarine sulcus, 3 mm thick. The parameters for the object and face localizers performed in the translations across quadrants experiment were the same as the functionals in the translations across quadrants experiment.

Retinotopic mapping experiments

To establish the spatial organization of the visual areas in the ventral and lateral surfaces of the occipito-temporal cortex, we measured activation produced by popular animated films played sequentially in a wedge-shaped aperture (Fig. 1). In the standard-resolution scans, the wedge-shaped apertures were displayed to the right, to the left, and above or below fixation. In the high-resolution scans, the wedge-shaped apertures were displayed at one of four locations relative to fixation along 45° diagonals: up-right; down-right; down-left; and up-left. In both experiments the wedge covered a 45° sector and its tip was displaced 1° from fixation, and subjects fixated centrally on a stationary dot. The area covered by the whole display was 30° vertically and 43° horizontally. The control condition was a blank dark screen with a fixation point. Unlike phase mapping techniques used in other retinotopic studies (Teo *et al.*, 1997; Wandell *et al.*, 2000; Larsson & Heeger, 2006), we used a control period in order to determine the location of peak activation for the UVF stimulation and compared that with the location of peak activation for LVF stimulation. The control condition and the mapping conditions lasted 16 s per epoch with 22 epochs per scan. For both experiments each run was repeated four times with different segments of the film. Subjects pressed a key when the movie switched from one animated film to a different animated film.

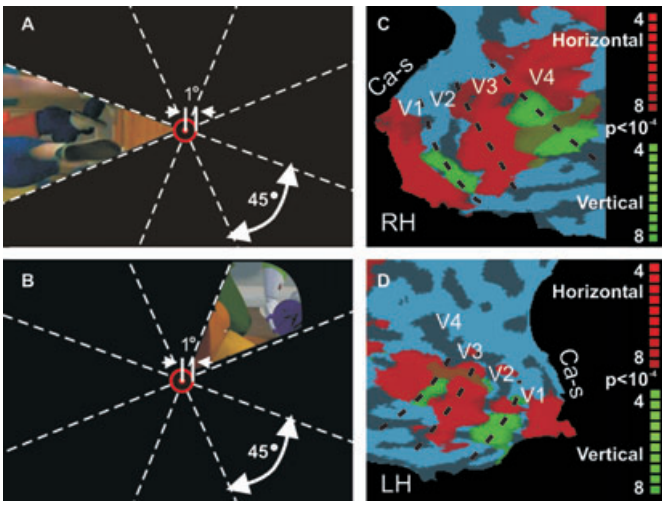

FIG. 1. In the retinotopic mapping experiment, subjects watched movies played in wedged-shaped apertures that appeared in one of four locations: (A) to the left or right, or above and below fixation in the standard-resolution scans; or (B) along 45 ° diagonals in the high-resolution scans. Activation from the retinotopic mapping experiments were plotted on flattened cortical maps for each subject, and the borders between the retinotopic areas were demarcated based on vertical and horizontal meridians. Maps (C) and (D) show cortical activation in the ventral occipital cortex of the right and left hemisphere for a single representative subject. Green areas represent activation to the UVF and red areas represent activation to the left visual field (C) and right visual field (D). Ca-s, calcarine sulcus.

Adaptation to translations across quadrants

Using a slow event-related design we measured adaptation to faces that moved between four quadrants in the visual field. The faces were modified in Adobe Photoshop into a round shape subtending a visual angle of approximately 6°. There were four locations in which a face could be presented: up-right; up-left; down-right; and down-left (Fig. 2B). In each trial the same face was presented sequentially in two different locations. There were four face translations: up-left to up-right; down-left to down-right; up-left to down-left; up-right to down-right. The faces were presented for 400 ms each with an interstimulus interval of 200 ms, and the intertrial interval was 11 s. A fixation dot was displayed during the entire trial and subjects were instructed to

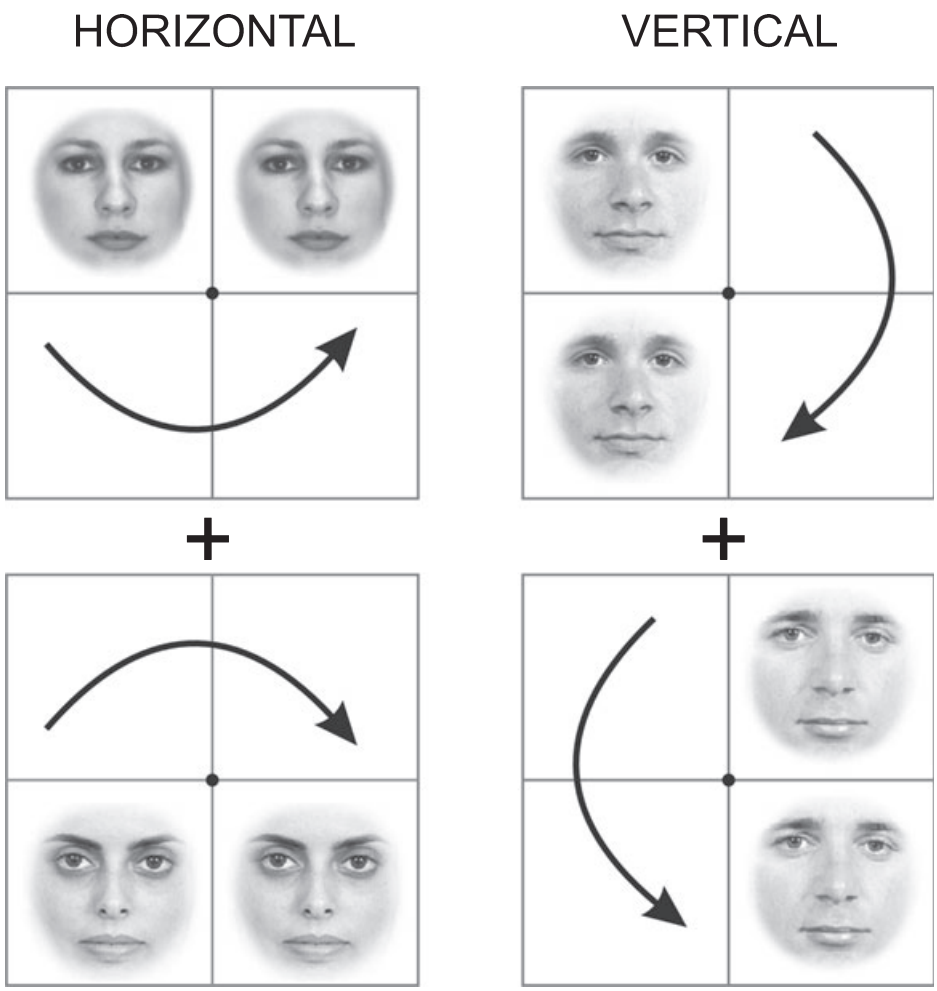

FIG. 2. Stimulus conditions for the translations across quadrants experiments. In each trial the same face was presented sequentially in two different locations as marked by the arrows. There were four face translations: up-left to up-right; up-left to down-left; up-right to down-right; down-left to down-right. Adaptation to vertical translations was calculated by summing the activations to vertical translation in both left and right visual fields. Adaptation to horizontal translations was calculated by summing activations to horizontal translations also in both UVF and LVF. The lines demarking the visual quadrants were not displayed during the experiment.

fixate on this dot. Subjects indicated with a key press whether the faces changed position horizontally or vertically. There were eight trials per face translation in each run and three runs in total. The order of the face translations was pseudo-randomized such that each combination of translations followed the others an equal number of times. As a measure of the degree of adaptation to vertical and horizontal translations, we summed the activation for both vertical translations and compared it with the sum of both horizontal translations. Note that each sum carried activation to faces presented in all four quadrants of the visual field, the only difference being the direction of translation.

Localizers

Object localizers. To identify object-sensitive brain regions we presented our subjects with intact 2D black and white line drawings of objects (animals, tools and letters) alternating with scrambled versions of the same images. Three functional scans were performed with 25 epochs per scan, and each epoch was 12 s long. Twelve images were presented in each epoch at 1-s intervals. To control for attention, subjects performed a one-back matching task where they pressed a response key whenever they saw two identical images, either intact or scrambled, in a row.

Object and face localizers. To identify face- and object-sensitive brain areas for the adaptation experiments, we presented subjects with intact 2D gray-scale photographs of faces, places and common everyday objects, which alternated with scrambled versions of the same images. Three functional scans were performed with 19 epochs per scan, and each epoch was 15 s long. Fifteen images were presented in each epoch at 1-s intervals. Subjects performed a one-back matching task as in the object localizer. Note that previous research has shown that LO is invariant to changes in picture format between line drawings and photographic images (Kourtzi & Kanwisher, 2000).

Image analysis and regions of interest (ROI)

Analysis was carried out using the Brain Voyager QX software. Three-dimensional statistical maps were calculated for each subject based on a general linear model. The representations of vertical and horizontal visual field meridians were mapped onto flattened cortical surfaces in each subject so that the borders between V1v, V2v, VP and V4v could be delineated (see Fig. 1C and D for details). We found UVF representation in V1, V2, VP and also within the boundaries of the Talairach coordinates for ventral ‘human V4′ (V4v) as defined by other researchers (Zeki *et al.*, 1991; McKeefry & Zeki, 1997;

Beauchamp *et al.*, 1999; Bartels & Zeki, 2000; Kastner *et al.*, 2000). Beyond this region, we did not observe UVF representation until LO. When the activity of the contralateral/LVF was plotted, we found a consistent pattern of activation, which lay adjacent and lateral to the UVF activation in V4v (Fig. 4). LO was defined as a set of contiguous voxels in the dorsal caudal region of LO that showed significantly stronger activation ($P < 10^{-4}$, uncorrected) to intact vs. scrambled line drawings of objects for the retinotopic mapping experiments. For the analysis of peak activation (Fig. 5), we selected the most significantly activated 27 voxels, the 'hotspot' of activity, within each region (V4v and LO).

In the translations across quadrants experiment, LO was defined as a set of contiguous voxels in the dorsal caudal region of LO that showed stronger activation ($P < 10^{-4}$, uncorrected) to intact vs. scrambled gray-scale photographic images of objects. FFA was defined as a set of contiguous voxels lying on the fusiform gyrus that showed significantly stronger activation to faces compared with objects and places ($P < 10^{-4}$, uncorrected). In the translations across quadrants experiment we sampled activation across the whole ROI in LO and FFA.

Results

Retinotopic mapping

In both retinotopic mapping experiments we found that peak activations to UVF and LVF displays overlapped in LO. In Fig. 3, we show maps of UVF and LVF activation in LO for a single representative subject from the high-resolution scans. The overlap in UVF and LVF representation was evident when we contrasted UVF and LVF against the control period. The areas of greatest activation, shaded in white, show a similar pattern. The highest peak for the UVF was at a location (indicated by the red square) that was not measurably different from the peak for LVF. The one difference is that the activation for LVF is higher and broader than that for UVF. A careful examination of Fig. 3 shows that there are small regions within LO that show a slight preference for either UVF or LVF stimulation. However, it should be noted that these regions are along the flanks, not at the peaks. The actual peaks of activation to UVF and LVF overlap.

To confirm that there was little difference in the spatial localization of peak activation for UVF and LVF, we compared the location of peaks in LO to those of V4v (Fig. 4). Separate analyses of the Talairach coordinates at peak activation were performed. In the standard-resolution scans we found a significant difference along the *x*-axis of the Talairach coordinate system in V4 (LH = $t_{1,9} = 4.8$, $P = 0.002$; RH = $t_{1,9} = 10.2$, $P < 0.001$). There were no reliable differences between the *y*-axis or *z*-axis coordinates ($t < 1$, RH and LH for *y* and *z*, respectively). It is clear from Fig. 4A that the majority of subjects showed a lateral shift between the UVF peak and the LVF peak in V4. Our finding of a clear and consistent topography in V4v replicates previous studies (McKeefry & Zeki, 1997; Bartels & Zeki, 1998, 2000; Zeki, 2001; Wade *et al.*, 2002). In comparison to V4v, the coordinates of peak activations to UVF and LVF stimulation in LO were more overlapping. Figure 4B shows that on average UVF and LVF peaks are in close proximity with no clear topographical organization. Statistically, this observation was borne out. We did not find reliable differences between the *x*, *y* and *z* coordinates. The results

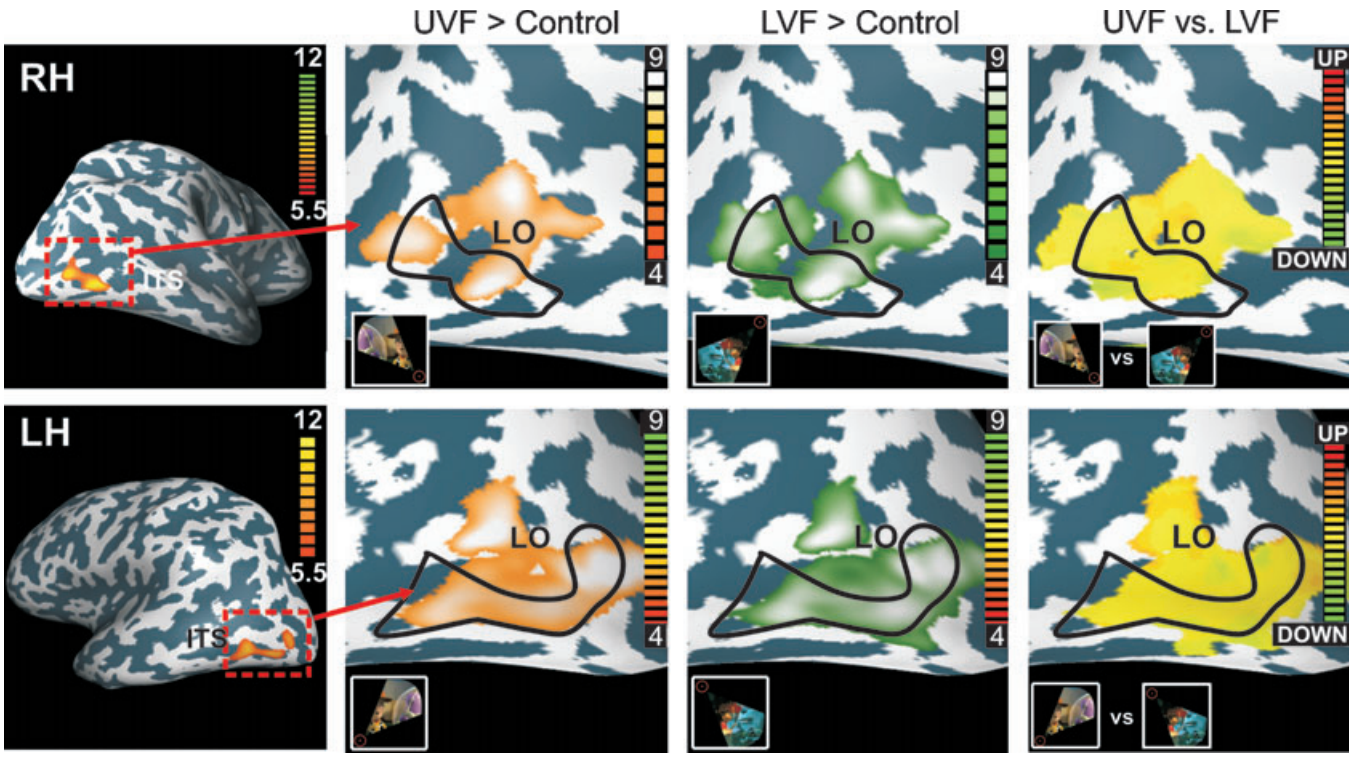

FIG. 3. The peaks of upper (UVF) and lower visual field (LVF) activation in the lateral occipital region (LO) from a single representative subject. Activation peaks are represented by increased brightness. For UVF and LVF activations contrasted with fixation, the peaks lie in the same location within the LO (black line). For UVF contrasted with LVF activation, the greatest differences do not lie on the peaks of activation but at the edges of LO. UVF (red) and LVF (green) activation was defined by contrasting [UVF vs. blank fixation] or [LVF vs. blank fixation], threshold: $P < 0.005$. The rightmost color maps show the relative contribution of UVF vs. LVF beta weights [(ßUp – ßDown)/(ßUp + ßDown)], ranging from red (UVF > LVF) to yellow (UVF = LVF) to green (LVF > UVF) for locations where at least one of the two predictors was significant at $r > 0.4$. Visual field activation was produced by using animated cartoon films played sequentially in a wedge-shaped aperture (see insets and Fig. 1), and LO was defined by contrasting intact vs. scrambled objects (threshold: $P < 0.001$). ITS, inferior temporal sulcus.

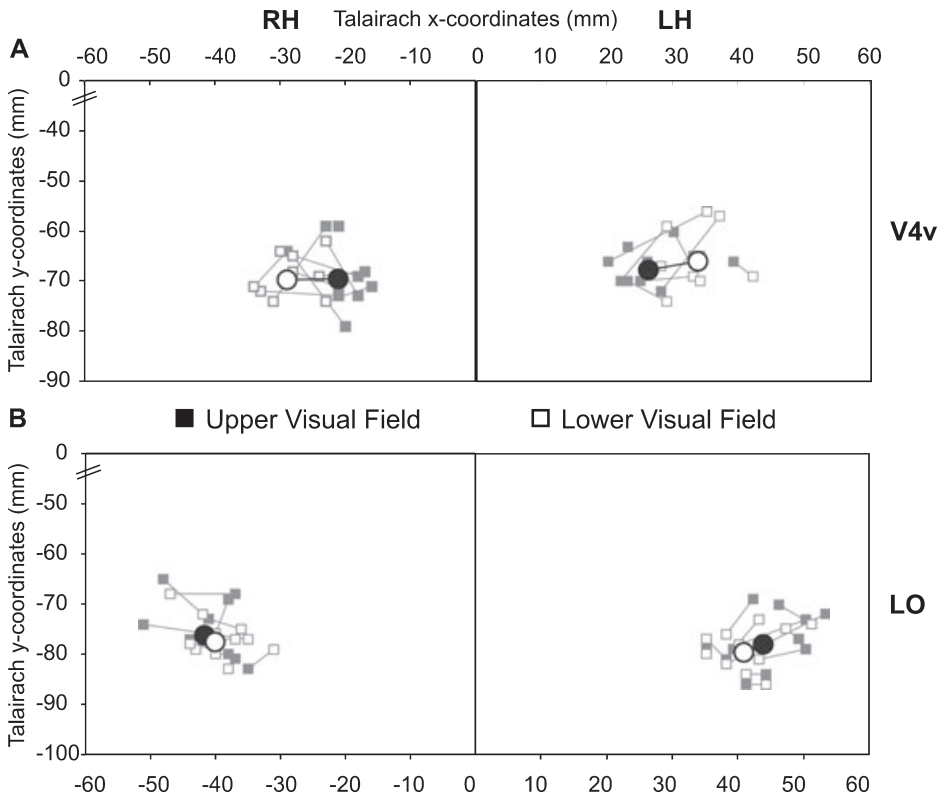

FIG. 4. Each subject's Talairach coordinates of peak upper visual field (UVF) activation (gray squares) and peak lower visual field (LVF) activation (white squares) taken from standard-resolution retinotopy mapping experiment. The UVF and LVF peaks lie in separate regions in V4v (A) but lie in overlapping regions in the lateral occipital region (LO, B). The gray lines link the peaks for each subject. The averaged coordinates are represented as black circles (UVF coordinates) and white circles (LVF coordinates), and show clearly that there is a lateral shift in both hemispheres in V4v. In contrast, peaks in LO lie in close proximity and there is no clear spatial relationship between them. RH, right hemisphere; LH, left hemisphere.

from the high-resolution scans were similar. For V4v in both left and right hemispheres there was a significant difference between the x Talairach coordinates of the activation peaks for UVF and LVF (LH = $t_{1,5} = 2.6$, $P < 0.05$; RH = $t_{1,5} = 4.29$, $P < 0.01$), but no reliable differences between UVF and LVF peaks in LO. Note that Talairach coordinates are not exact measures of cortical location as they introduce anatomical distortions, and there is considerable subject- to-subject variability in both UVF and LVF locations as depicted in Fig. 4. But, the difference in location, across individual subjects, is consistently in the same direction in V4v and in random locations in LO.

An important consideration is the relationship between peak localization and artifacts associated with large draining veins. If the peaks we sampled in LO corresponded to large vein artifacts it might obscure retinotopic organization because the corresponding BOLD signal could be pooling activity from larger regions of cortex that include both the upper and lower field representations. To address this problem we ran the data set from the high-resolution scans through a vessel suppression algorithm developed by Menon (2002), which suppresses the BOLD effect from larger veins. As with the original data, we did not find any reliable differences between the peaks for UVF and LVF activation in LO (LH: x coordinates, $t < 1$, y coordinates, $t_{1,7} = 1.104$, $P = 0.31$, z coordinates, $t < 1$; RH: x coordinates, $t_{1,7} = 1.87$, $P = 0.10$, y coordinates, $t_{1,7} = 1.426$, $P = 0.19$, z coordinates, $t < 1$). The analyses of the Talairach coordinates suggest that the UVFs and LVFs are represented in the LO by similar populations of neurons.

In the standard-resolution and high-resolution scans we found the peak of the UVF activation and the peak of LVF activation and compared the fMRI response to stimulation by both UVF and LVF at these peaks (Fig. 5). In this analysis, we used half of the data set to localize the peaks for UVF and LVF activation in LO and V4v, and the other half to calculate the % signal change in each region. The peaks were selected as the most significantly activated 27 voxels, the 'hotspot' of activity, within each region (V4v and LO). In V4v, we found that UVF and LVF information was not integrated (Fig. 5A and C). In regions that showed a preference for UVF, there was little activation for LVF (high resolution: $t_{1,7} = 5.151$, $P = 0.001$; standard resolution: $t_{1,10} = 6.724$, $P < 0.0001$). In regions that showed a preference for LVF there was less activation for UVF (high resolution: $t_{1,6} = 3.66$, $P = 0.01$; standard resolution: $t_{1,10} = 5.86$, $P = 0.0002$). Also, in V4v, there was greater activation to UVF stimulation than LVF in the standard-resolution data ($F_{1,10} = 7.47$, $P = 0.02$). When comparing the peak activations to UVF and LVF stimulation for LO (Fig. 5B and D), we found that, unlike V4v, there were no reliable differences in regions that showed a preference for UVF (high resolution: $t_{1,7} = 1.7$, $P = 0.13$; standard resolution: $t < 1$). Similarly, in regions that showed a preference for LVF the differences were not significant, but there was a trend towards higher activation for LVF compared with UVF stimulation (high resolution: $t_{1,7} = 2.18$, $P = 0.07$; standard resolution: $t_{1,10} = 1.72$, $P = 0.12$).

To summarize, in the retinotopic mapping experiments we found distinct regions in V4v representing UVF and LVF in the contralateral hemifield. Higher up the visual processing stream, in LO, we found

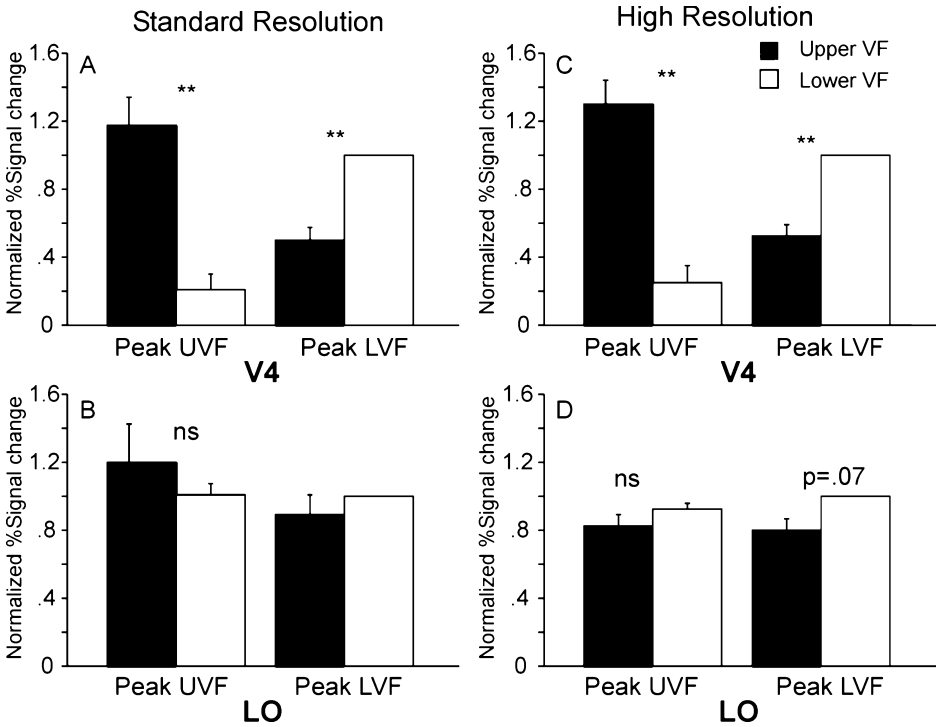

FIG. 5. Averaged response at the location of peak activation to upper (UVF) and lower visual field (LVF) stimulation in V4v and the lateral occipital region (LO; data from the standard- and high-resolution retinotopy experiments, collapsed across hemispheres). (A and C) UVF (black bars) and LVF (white bars) responses at the peaks in V4v. (B and D) UVF and LVF responses at the peaks in the LO. Note that the UVF activation profile in V4v shows little contribution from LVF, whereas in the LO, UVF and LVF activation is about the same. The opposite pattern is present in the LVF activation profile in V4v. LO also shows less of a contribution from UVF. The pattern is consistent across standard- and high-resolution data sets. For each subject and in each hemisphere, fMRI % signal change was measured at two different statistical peaks within LO: UVF peak > fixation; LVF peak > fixation. The resulting data were then normalized to the level of LVF activation at the peak of LVF > fixation for ease of comparison, and averaged across subjects and hemispheres (*P = 0.01, **P = 0.001).

evidence of overlapping activation maps for UVFs and LVFs. The results suggest that LO may be the first point along the ventral visual pathway in which information converges within a hemifield.

Translations across quadrants

The data from the retinotopic mapping experiments indicated that the same regions in LO coded both the upper and lower contralateral fields. To determine if the same population of neurons was generating this activation, we conducted an fMRI adaptation experiment. In this experiment we wanted to compare LO with a region where, *a priori*, we had reason to expect that there would be no difference between horizontal and vertical fMRI adaptation effects. Our choice of FFA as a comparison region involved a number of factors. Firstly, we needed a region that would adapt to both horizontal and vertical translations because it had sufficiently large receptive fields. Grill-Spector's works (Grill-Spector *et al.*,1999; Grill-Spector & Malach, 2001) on fMRI adaptation showed that posterior fusiform sulcus (pFs; or LOa), a ventral anterior subdivision of the LOC, was position invariant, and should therefore adapt to stimuli that translated across the visual field. However, pilot data suggested that pFs, like LO, had a contralateral preference that made it an unsuitable candidate. Because FFA is located anterior to pFs, and was reported as non-retinotopic (Lerner *et al.*, 2001), we thought it would make a good candidate region to compare against LO. Secondly, fMRI adaptation effects are reliably found in both LO and FFA across a variety of stimulus parameters (Kourtzi & Grill-Spector, 2005). We felt that V4v was a less suitable candidate for comparison with LO because fMRI adaptation has not been studied as extensively in V4v and adaptation effects in retinotopic regions are less reliable (Murray *et al.*, 2006). This would make interpreting a null finding (i.e. no difference between vertical and horizontal translations) more difficult as it could be due to methodological limitations rather than neuronal properties.

In this translations across quadrants experiment, the same stimulus sets (with equal numbers of stimuli in each of four quadrants) were presented but paired within hemifields or between hemifields. We contrasted within- and between-hemifield adaptation for identical sets of stimuli so that each analysis included activation from all four visual fields, the difference being that the faces either translated horizontally or vertically. The logic here was that if neurons in LO code the whole contralateral hemifield, there should be greater adaptation to repeated stimuli within a hemifield than to repeated stimuli across the two hemifields. Conversely, if LO consists of neurons that coded independently for UVF and LVF then we would expect comparable levels of activation for within- and between-hemifield conditions. The fMRI adaptation technique also circumvents the potential problem of large draining veins: if the results of the retinotopic mapping experiments were simply due to the response of veins that pool blood from both UVF and LVF representations, then we would also predict no differences between within- and between-hemifield conditions.

Figure 6A shows the fMRI response in left and right LO to faces that translated across the four visual quadrants. In left LO the fMRI response was higher to faces that moved up and down in the right hemifield compared with the left hemifield ($t_{1,12}$ = 3.9, P = 0.002). In right LO the fMRI response was higher to faces that moved up and down in the left hemifield compared with the right hemifield ($t_{1,12}$ = 2.4, P = 0.03). The results showed a clear contralateral

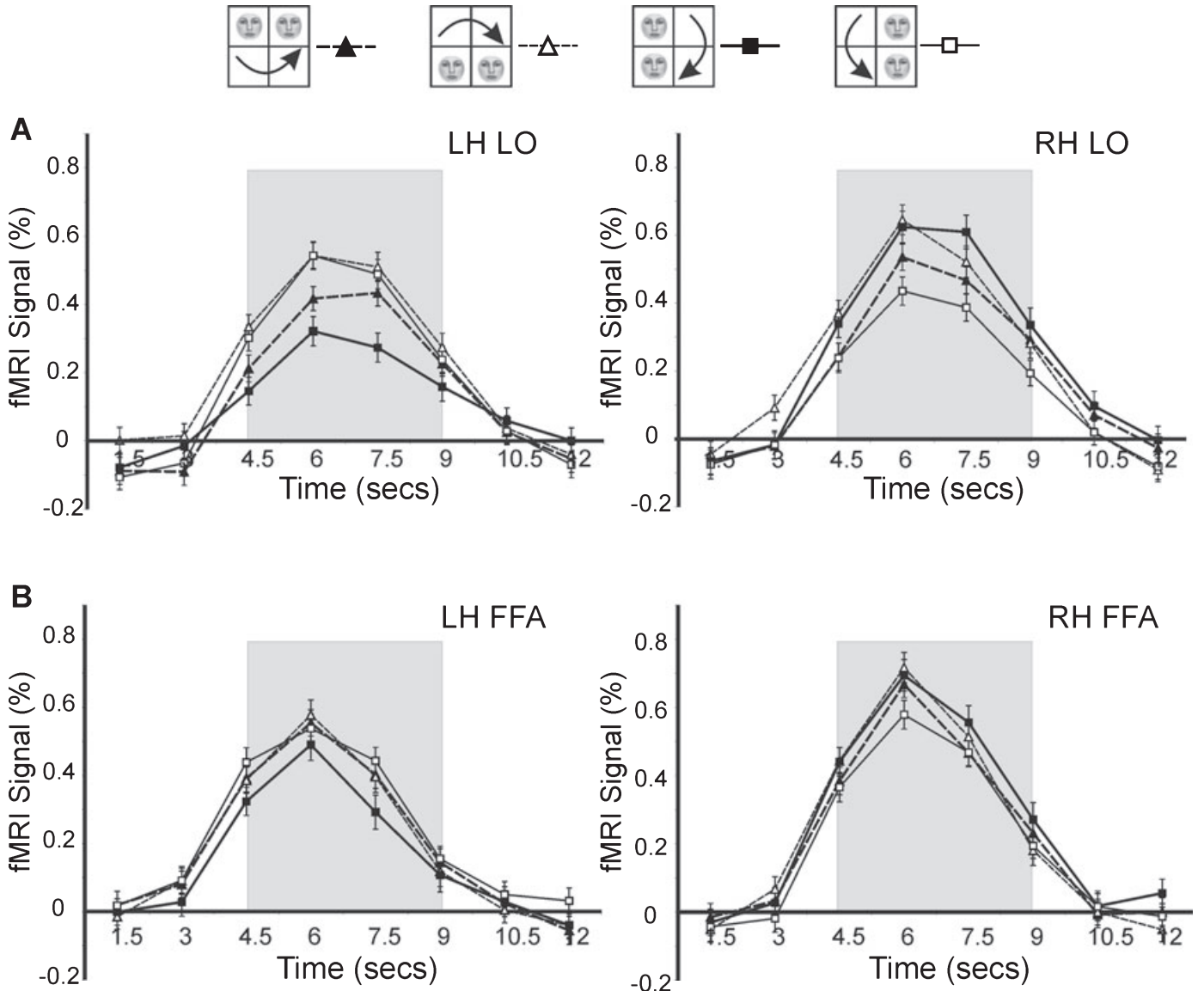

FIG. 6. Average time course of brain activation to translations between four quadrants of the visual field. (A) Time courses for left (LH) and right (RH) hemispheres of the lateral occipital region (LO). In the right LO there is greater activation to translations in the left visual field (solid line, black square); in the left LO there is greater activation to the right visual field (solid line, white square), showing a clear contralateral preference. There is also more activation to translations made in the LVF compared with the UVF. (B) Time courses for left and right hemispheres of the fusiform face region (FFA). In both the right and left FFA there is clearly less of a distinction between the four quadrants of the visual field compared with the LO. There is, however, some suggestion of a contralateral preference in the FFA (see text for details). fMRI, functional magnetic resonance imaging.

preference in LO. There was also more activation to faces that translated position from left to right in the LVF compared with the UVF ($t_{1,12} = 2.89$, $P = 0.01$). In Fig. 6B the fMRI response in the left and right FFA is shown. There was more activation in the left FFA to faces that translated up and down in the right visual field compared with the left visual field ($t_{1,12} = 2.5$, $P = 0.01$). In the right FFA there was a trend for more activation to faces that translated up and down in the left visual field compared with the right visual field ($t_{1,12} = 1.45$, $P = 0.08$). Interestingly, the data suggest that in the FFA there was a small contralateral preference, which is contrary to what we expected.

To determine whether neuronal populations in LO and FFA code for both the UVF and LVF, we averaged the activation for faces translating from left and right in both the UVF and LVF (from Fig. 2 – Quadrants [1,2] + [3,4]), and we contrasted these measurements with the summed activations for faces translated up and down in both the left and right visual fields (from Fig. 2 – Quadrants [1,3] + [2,4]). On the one hand, if all quadrants showed the same adaptation or no adaptation, the two sums would be equal. On the other hand, if neurons in LO or FFA code for both the UVF and LVF, then we would expect more adaptation for faces translating up and down compared with left and right; that is, there would be a greater fMRI response to horizontal translations compared with vertical translations. In Fig. 7A, it is clear that in LO, faces translating from left to right produced more activation than faces translating up and down. A 2×2 ANOVA with factors of Hemisphere (right/left) and Translation (vertical/horizontal) performed on the summed fMRI response showed a main effect of Translation ($F_{1,8} = 5.5$, $P = 0.03$). One-tailed t-tests showed more adaptation to vertical translations compared with horizontal

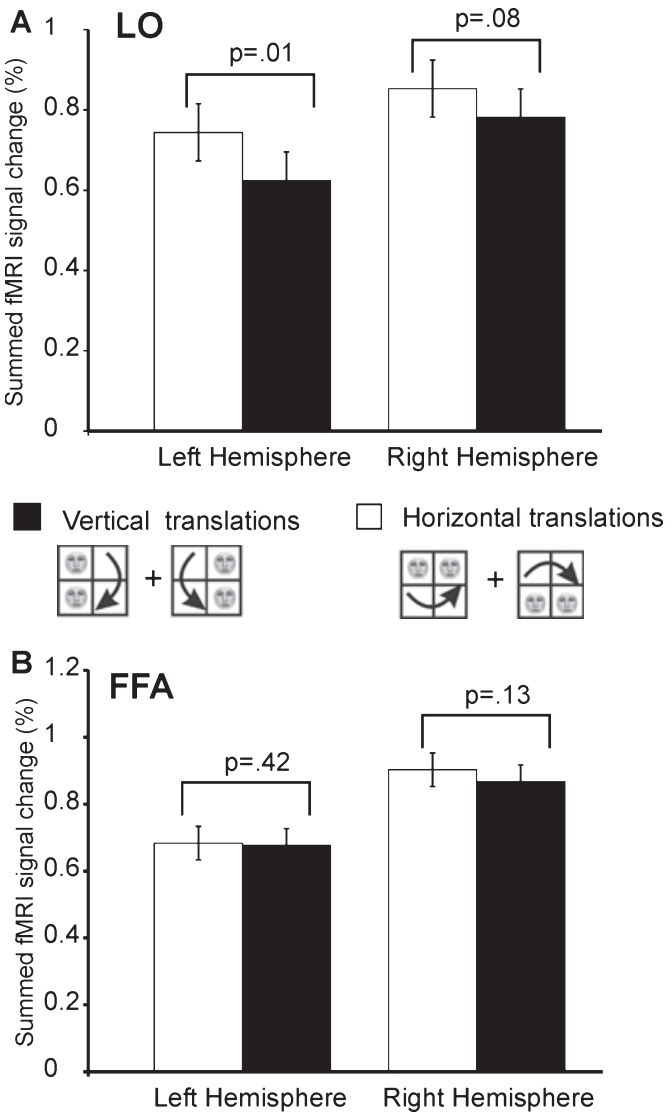

FIG. 7. Translations of faces between UVF and LVF produced more adaptation than translations from left to right visual fields in the lateral occipital region (LO) but not in the fusiform face region (FFA). Identical faces were translated from vertical and horizontal quadrants, as in Fig. 3. (A) Summed activation for horizontal translations (white bars) and vertical translations (black bars) in the left (LH) and right (RH) LO. (B) Summed activation for horizontal and vertical translations in the left and right FFA. fMRI, functional magnetic resonance imaging.

translations in left LO ($t_{1,12}$ = 2.8, P = 0.01), and a trend in the same direction in right LO ($t_{1,12}$ = 1.5, P = 0.08). In Fig. 7B it appears that the FFA is showing a trend in the same direction as LO; however, this was not supported statistically. A 2 × 2 ANOVA with factors of Hemisphere (right/left) and Translation (vertical/horizontal) produced no effects for Translation or Hemisphere.

To determine that subjects were able to maintain eye fixation we also examined the pattern of activation in V1/V2. The region V1/V2 was defined functionally by contrasting activation to faces translated in the UVF with activation to faces translated in the LVF and anatomically as regions lying above or below the calcarine sulcus. All subjects showed UVF activation below the calcarine sulcus and LVF activation above the calcarine sulcus in the right hemisphere (false discovery rate threshold < 0.05). In the left hemisphere 11 subjects showed a similar pattern of activation (false discovery rate threshold < 0.05). Two subjects only showed activation below the calcarine sulcus to UVF stimulation. For each subject we sampled the level of activation in left and right V1/V2 produced by faces translated in the left and right visual fields. In the left V1/V2 there was more activation to the faces translating in the right visual field compared with the left visual field ($t_{1,12}$ = 3.51, P = 0.004), and in the right V1/V2 there was more activation to faces translated in the left visual field compared with the right visual field ($t_{1,12}$ = 2.99, P = 0.01). The data indicated that subjects were able to maintain fixation during the translation across quadrants experiment.

Discussion

Our results suggest that the transition from small receptive fields in the early retinotopic areas to larger receptive fields in the higher order regions such as LO (Kastner *et al.*, 2001) are accompanied by a merger of the upper and lower visual quarter-fields within each hemisphere as one progresses through the visual hierarchy. In our retinotopic mapping experiments we found that the early ventral visual areas (V1v, V2v and VP) were clearly selective for the contralateral UVF. The first evidence of LVF representation in the ventral cortex was in V4v where we found two distinct regions showing a preference for either UVF stimulation or LVF stimulation. In line with other studies, our data suggest that in V4v there are independent populations of neurons representing UVF and LVF, and that V4v as a whole represents a full hemifield.

In LO the picture is quite different. We found overlapping regions responding both to UVF and LVF stimulation, and a clear contralateral preference with greater activation to left and right LVFs. The data suggest that the receptive fields of neurons in LO cover both UVF and LVF. In support of this claim, we found there was greater adaptation to vertical translations of faces than horizontal translations. Thus, LO combines the vertical, within-hemisphere features of an object leaving it to downstream structures to combine the left and right, across-hemisphere features. In the FFA we found no reliable difference in adaptation to vertical and horizontal translations of faces, suggesting that neurons in the FFA integrate information from across both hemifields. However, there was evidence of a contralateral preference in the FFA, suggesting that there are neurons within this region that show similar properties to neurons in LO.

Our results differ somewhat from those reported by Grill-Spector *et al.* (1999). They used fMRI adaptation techniques to compare activation of static different and identical faces translated to different positions in the visual field. They found no adaptation to translated faces in LO, suggesting that neurons in LO were not position invariant, whereas we found evidence of adaptation to vertical translations relative to horizontal translations. This difference in results can be explained by differences in methodology. Grill-Spector *et al.*'s design did not allow for separate analyses of translations within the same hemifield compared with translations across hemifields. In addition, as we did not include a 'no translation' condition in our adaptation experiment we cannot report on the size of the adaptation effect for vertical translations relative to repeated position and identity. However, the lack of a no translation condition does not undermine our findings regarding adaption to vertical and horizontal translations. There are four possible outcomes regarding the response of LO to stimulus translations: (i) no position invariance, in which case there would be no adaptation for either vertical or horizontal translations; (ii) position invariance, with equal effects of adaptation to vertical and

horizontal translations; (iii) position tuning with more adaptation along a continuum ranging from no translation to cross-hemifield translation; (iv) position invariance within a hemifield. The results of the adaptation experiment show a contralateral preference, which eliminates outcome (i) and that effects of adaptation are not equal for vertical and horizontal translations, which eliminates outcome (ii). With the current design, we cannot distinguish between outcomes (iii) and (iv), but the results from the adaptation experiment combined with the mapping experiments would suggest that a significant proportion of neurons in LO have receptive fields that cover both UVF and LVF.

In contrast to LO, the FFA showed little or no difference in the adaptation rates to vertical and horizontal translations, suggesting that neurons in this region integrate information from all four quadrants of the visual field. Grill-Spector *et al.* (1999) also found evidence of adaptation to translations in a region named LOa (located anterior and ventral to LO, also called pFs for its location in the posterior fusiform sulcus). Taken together these results suggest that in these more anterior/ventral regions of object-sensitive cortex the right–left organization is devolving. It is likely that the receptive field sizes of neurons in this region are sufficient to integrate information across large portions of the visual field. This picture of the FFA is somewhat simplified though, as we also found evidence of a contralateral preference in the FFA in the translations across quadrants experiment, replicating a recently reported contralateral preference in the FFA by Hemond *et al.* (2007). Although the contralateral preference we found in the FFA was much smaller than in LO, it does suggest that there are neurons in the FFA that distinguish between the hemifields. In support there is neurophysiological evidence from macaques that high-level ventral regions involved in object recognition may be less position tolerant than traditionally thought based on their receptive field sizes (DiCarlo & Maunsell, 2003). For example, it has been shown that neurons in the inferior temporal region show a gradual decrease in their response the further away an image is presented from the neuron's RF center (Desimone *et al.*, 1984; Boussaoud *et al.*, 1991; Op De Beeck & Vogels, 2000).

Interestingly, our results contrast with those recently reported by Larsson & Heeger (2006). Using a phase mapping technique they reported two visual field maps (LO1 and LO2) with distinct contralateral and UVF and LVF representations. It is possible that the conflicting results are due to methodological differences. Firstly, we used movies containing a wealth of objects whereas they used a flashing texture pattern. Our movies would be a much more potent stimulus for activating LO (mostly likely the LO2 region reported by Larsson and Heeger). Secondly, our stimuli ($30\,^\circ \times 43\,^\circ$) subtended a much larger visual angle than did Larsson and Heeger's ($6\,^\circ$). It is possible, though unlikely, that the integration within hemifields differs between the central and peripheral representations. Thirdly, we used meridian mapping techniques, and Larsson and Heeger used phase mapping techniques. We believe that phase mapping techniques are suited to detecting small differences in activation levels and they discriminate between the non-overlapping regions, which we observed using meridian mapping. It should be noted, however, that these non-overlapping regions do not occur at the peaks. They occur in the valleys and edges of activation clusters, that is, regions that do not respond maximally to objects in the UVF or LVF. In comparison, the location of peak differences between UVF and LVF activation in V4v lie at the peaks contrasted against the control. This suggests that LO may contain a mixed population of neurons; some respond to both LVF and UVF stimulation; some respond more exclusively to UVF or LVF stimulation. Indeed, Larsson and Heeger noted that there was a great deal of intersubject variability in the retinotopy of LO1 and LO2. In their study, 46% of subjects had UVF and LVF representations that corresponded to full hemifields, 30% of subjects had visual field representations that were closer to quadrants and the remaining 23% the visual field topography was indistinct. The important point from our findings is that the neurons that are maximally activated in LO by objects are those neurons that integrate information from both UVF and LVF.

Our findings may also explain why cross-hemispheric tasks, such as perceptual illusory contour completion (Pillow & Rubin, 2002) and tasks that involve splitting attention between different locations in the visual field (McMains & Somers, 2004; Alvarez & Cavanagh, 2005; Kraft *et al.*, 2005), are performed more poorly across the vertical meridian compared with presentations within the same hemifield. Based on their findings, Pillow & Rubin (2002) argued that illusory contour completion must occur in the early visual areas because: (i) higher order visual regions like the LOC respond preferentially to objects; (ii) information about objects often spans across hemifields; and (iii) therefore interhemispheric transfer must be more efficient. Our findings support an alternative explanation. If, as our data indicate, neurons in LO code for UVF and LVF, this might facilitate detection of illusory contours within a hemifield. But illusory contours that cross hemifields would require combining information across hemispheres, resulting in a decrement in performance. This explanation also accords with evidence of a strong response in the LOC to illusory contours (Mendola *et al.*, 1999; Murray *et al.*, 2002; Pegna *et al.*, 2002; Stanley & Rubin, 2003).

Finally, an interesting finding was that in both retinotopic mapping experiments and in the fMRI adaptation experiments we found higher activation to LVF displays in LO. This finding has been reported elsewhere (Grill-Spector *et al.*, 1999; Niemeier *et al.*, 2005). LVF advantages have been observed in a variety of perceptual tasks, such as global form perception (Christman, 1993), the perception of illusory conjunctions (Rubin *et al.*, 1996) and color discrimination (Levine & McAnany, 2005), as well as visuo-motor tasks (see Danckert & Goodale, 2003 for a review). Some LVF advantages may be due to the greater proportion of ganglion cells in superior retina. But high-level visual processing, like the perception of illusory conjunctions, most certainly requires cortical involvement and may be explained in part by the properties of neurons in LO. Alternatively, it has been suggested that LVF advantages are due to a finer resolution of attention (He *et al.*, 1996). Although, in general, the fMRI response is sensitive to levels of attentional arousal, the tasks described in the preceding experiments did not require more effort for stimuli displayed in the LVF compared with the UVF. Indeed, subjects may have benefited from a wide spread of attention, particularly in the translations across quadrants experiment, where they had to indicate whether a face translated horizontally or vertically. However, as we only controlled for attentional arousal, not attentional resolution, further research is necessary to distinguish whether the LVF preference we observed in LO is due to attentional resolution or is a general property of neurons in LO.

To conclude, the retinotopic mapping and fMRI adaptation experiment demonstrated that neurons in LO have overlapping representations for UVF and LVF, and preferentially respond to stimuli presented in the contralateral hemifield. The results suggest that LO may be the first point along the ventral visual pathway in which information converges within a hemifield. We speculated that the receptive field organization in LO may account for behavioral findings of greater integration within than between hemifields for

contour completion, and greater difficulty in splitting attention within a hemifield than across the vertical meridian.

Acknowledgements

We would like to thank Dr Herb Goltz, Joy Williams, Joe Gati, and Jeff Mason from the Robarts Research Institute London, Ontario, Canada, for their help and advice in collecting the imaging data. Mary-Ellen Large is currently affiliated with the University of Hull, UK.
This work was supported by an award from the Canadian Institutes of Health Research award to T. Vilis, a Natural Sciences and Engineering Research Council of Canada operating grant to J. Culham, and a Natural Sciences and Engineering Research Council Undergraduate Student Research Award (USRA) to Anil Kuchinad.

Abbreviations

BOLD, blood oxygen level dependent; FFA, fusiform face region; fMRI, functional magnetic resonance imaging; LO, lateral occipital region; LOC, lateral occipital complex; LVF, lower visual field; pFs, posterior fusiform sulcus; ROI, region of interest; UVF, upper visual field.

References

Alvarez, G.A. & Cavanagh, P. (2005) Independent resources for attentional tracking in the left and right visual hemifields. *Psychol. Sci.*, **16**, 637–643.

Bartels, A. & Zeki, S. (1998) The theory of multistage integration in the visual brain. *Proc. Biol. Sci.*, **265**, 2327–2332.

Bartels, A. & Zeki, S. (2000) The architecture of the colour centre in the human visual brain: new results and a review. *Eur. J. Neurosci.*, **12**, 172–193.

Beauchamp, M.S., Haxby, J.V., Jennings, J.E. & DeYoe, E.A. (1999) An fMRI version of the Farnsworth-Munsell 100-Hue test reveals multiple color-selective areas in human ventral occipitotemporal cortex. *Cereb. Cortex*, **9**, 257–263.

Boussaoud, D., Desimone, R. & Ungerleider, L.G. (1991) Visual topography of area TEO in the macaque. *J. Comp. Neurol.*, **306**, 554–575.

Christman, S.D. (1993) Local-global processing in the upper versus lower visual fields. *Bull. Psychon. Soc.*, **31**, 275–278.

Danckert, J. & Goodale, M.A. (2003) Ups and downs in the visual control of action. In Johnson-Frey, S.H. (Ed.) *Taking Action: Cognitive Neuroscience Perspectives on Intentional Acts*. MIT Press, Cambridge, pp. 29–64.

Desimone, R., Albright, T.D., Gross, C.G. & Bruce, C. (1984) Stimulus-selective properties of inferior temporal neurons in the macaque. *J. Neurosci.*, **4**, 2051–2062.

DeYoe, E.A., Carman, G.J., Bandettini, P., Glickman, S., Wieser, J., Cox, R., Miller, D. & Neitz, J. (1996) Mapping striate and extrastriate visual areas in human cerebral cortex. *Proc. Natl Acad. Sci. USA*, **93**, 2382–2386.

DiCarlo, J.J. & Maunsell, J.H. (2003) Anterior inferotemporal neurons of monkeys engaged in object recognition can be highly sensitive to object retinal position. *J. Neurophysiol.*, **89**, 3264–3278.

Dougherty, R.F., Koch, V.M., Brewer, A.A., Fischer, B., Modersitzki, J. & Wandell, B.A. (2003) Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *J. Vis.*, **3**, 586–598.

Fox, P.T., Miezin, F.M., Allman, J.M., Van Essen, D.C. & Raichle, M.E. (1987) Retinotopic organization of human visual cortex mapped with positron-emission tomography. *J. Neurosci.*, **7**, 913–922.

Grill-Spector, K. & Malach, R. (2001) fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol. (Amst.)*, **107**, 293–321.

Grill-Spector, K. & Malach, R. (2004) The human visual cortex. *Annu. Rev. Neurosci.*, **27**, 649–677.

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

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

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

He, S., Cavanagh, P. & Intriligator, J. (1996) Attentional resolution and the locus of visual awareness. *Nature*, **383**, 334–337.

Hemond, C.C., Kanwisher, N.G. & Op de Beeck, H.P. (2007) A preference for contralateral stimuli in human object- and face-selective cortex. *PLoS ONE*, **2**, e574.

Kastner, S., De Weerd, P. & Ungerleider, L.G. (2000) Texture segregation in the human visual cortex: a functional MRI study. *J. Neurophysiol.*, **83**, 2453–2457.

Kastner, S., De Weerd, P., Pinsk, M.A., Elizondo, M.I., Desimone, R. & Ungerleider, L.G. (2001) Modulation of sensory suppression: implications for receptive field sizes in the human visual cortex. *J. Neurophysiol.*, **86**, 1398–1411.

Kourtzi, Z. & Grill-Spector, K. 2005. MRI adaptation: a tool for studying visual representations in the primate brain. In Rhodes, G. & Clifford, C.W.G. (eds), *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision*. Oxford University Press, Oxford, pp. 173–188.

Kourtzi, Z. & Huberle, E. (2005) Spatiotemporal characteristics of form analysis in the human visual cortex revealed by rapid event-related fMRI adaptation. *NeuroImage*, **28**, 440–452.

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

Kraft, A., Muller, N.G., Hagendorf, H., Schira, M.M., Dick, S., Fendrich, R.M. & Brandt, S.A. (2005) Interactions between task difficulty and hemispheric distribution of attended locations: implications for the splitting attention debate. *Brain Res.*, **24**, 19–32.

Large, M.E., Aldcroft, A. & Vilis, T. (2005) Perceptual continuity and the emergence of perceptual persistence in the ventral visual pathway. *J. Neurophysiol.*, **93**, 3453–3462.

Large, M.E., Aldcroft, A. & Vilis, T. (2007) Task-related laterality effects in the lateral occipital complex. *Brain Res.*, **1128**, 130–138.

Larsson, J. & Heeger, D.J. (2006) Two retinotopic visual areas in human lateral occipital cortex. *J. Neurosci.*, **26**, 13128–13142.

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

Levine, M.W. & McAnany, J.J. (2005) The relative capabilities of the upper and lower visual hemifields. *Vis. Res.*, **45**, 2820–2830.

Malach, R., Reppas, J.B., Benson, R.R., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R. & Tootell, R.B. (1995) Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc. Natl Acad. Sci. USA*, **92**, 8135–8139.

McKeefry, D.J. & Zeki, S. (1997) The position and topography of the human colour centre as revealed by functional magnetic resonance imaging. *Brain*, **120**(Pt 12), 2229–2242.

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

McMains, S.A. & Somers, D.C. (2004) Multiple spotlights of attentional selection in human visual cortex. *Neuron*, **42**, 677–686.

Mendola, J.D., Dale, A.M., Fischl, B., Liu, A.K. & Tootell, R.B. (1999) The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *J. Neurosci.*, **19**, 8560–8572.

Menon, R.S. (2002) Postacquisition suppression of large-vessel BOLD signals in high-resolution fMRI. *Magn. Reson. Med.*, **47**, 1–9.

Murray, M.M., Wylie, G.R., Higgins, B.A., Javitt, D.C., Schroeder, C.E. & Foxe, J.J. (2002) The spatiotemporal dynamics of illusory contour processing: combined high-density electrical mapping, source analysis, and functional magnetic resonance imaging. *J. Neurosci.*, **22**, 5055–5073.

Murray, S.O., Olman, C.A. & Kersten, D. (2006) Spatially specific FMRI repetition effects in human visual cortex. *J. Neurophysiol.*, **95**, 2439–2445.

Niemeier, M., Goltz, H.C., Kuchinad, A., Tweed, D.B. & Vilis, T. (2005) A contralateral preference in the lateral occipital area: sensory and attentional mechanisms. *Cereb. Cortex*, **15**, 325–331.

Op De Beeck, H. & Vogels, R. (2000) Spatial sensitivity of macaque inferior temporal neurons. *J. Comp. Neurol.*, **426**, 505–518.

Pegna, A.J., Khateb, A., Murray, M.M., Landis, T. & Michel, C.M. (2002) Neural processing of illusory and real contours revealed by high-density ERP mapping. *Neuroreport*, **13**, 965–968.

Pillow, J. & Rubin, N. (2002) Perceptual completion across the vertical meridian and the role of early visual cortex. *Neuron*, **33**, 805–813.

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

Schneider, W., Noll, D.C. & Cohen, J.D. (1993) Functional topographic mapping of the cortical ribbon in human vision with conventional MRI scanners. *Nature*, **365**, 150–153.

Sereno, M.I., Dale, A.M., Reppas, J.B., Kwong, K.K., Belliveau, J.W., Brady, T.J., Rosen, B.R. & Tootell, R.B. (1995) Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, **268**, 889–893.

Stanley, D.A. & Rubin, N. (2003) fMRI activation in response to illusory contours and salient regions in the human lateral occipital complex. *Neuron*, **37**, 323–331.

Teo, P.C., Sapiro, G. & Wandell, B.A. (1997) Creating connected representations of cortical gray matter for functional MRI visualization. *IEEE Trans. Med. Imaging*, **16**, 852–863.

Tootell, R.B. & Hadjikhani, N. (2001) Where is 'dorsal V4' in human visual cortex? Retinotopic, topographic and functional evidence *Cereb. Cortex*, **11**, 298–311.

Tootell, R.B., Mendola, J.D., Hadjikhani, N.K., Liu, A.K. & Dale, A.M. (1998) The representation of the ipsilateral visual field in human cerebral cortex. *Proc. Natl Acad. Sci. USA*, **95**, 818–824.

Wade, A.R., Brewer, A.A., Rieger, J.W. & Wandell, B.A. (2002) Functional measurements of human ventral occipital cortex: retinotopy and colour. *Philos. Trans. R Soc. Lond. B Biol. Sci.*, **357**, 963–973.

Wandell, B.A., Chial, S. & Backus, B.T. (2000) Visualization and measurement of the cortical surface. *J. Cogn. Neurosci.*, **12**, 739–752.

Wandell, B.A., Brewer, A.A. & Dougherty, R.F. (2005) Visual field map clusters in human cortex. *Philos. Trans. R Soc. Lond. B Biol. Sci.*, **360**, 693–707.

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

Zeki, S., Watson, J.D., Lueck, C.J., Friston, K.J., Kennard, C. & Frackowiak, R.S. (1991) A direct demonstration of functional specialization in human visual cortex. *J. Neurosci.*, **11**, 641–649.