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Functional measurements of human ventral occipital cortex: retinotopy and colour

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Human colour vision originates in the cone photoreceptors, whose spatial density peaks in the fovea and declines rapidly into the periphery. For this reason, one expects to find a large representation of the cone-rich fovea in those cortical locations that support colour perception. Human occipital cortex contains several distinct foveal representations including at least two that extend onto the ventral surface: a region thought to be critical for colour vision. To learn more about these ventral signals, we used functional magnetic resonance imaging to identify visual field maps and colour responsivity on the ventral surface. We found a visual map of the complete contralateral hemifield in a 4 cm^2 region adjacent to ventral V3; the foveal representation of this map is confluent with that of areas V1/2/3. Additionally, a distinct foveal representation is present on the ventral surface situated 3–5 cm anterior from the confluent V1/2/3 foveal representations. This organization is not consistent with the definition of area V8, which assumes the presence of a quarter field representation adjacent to V3v. Comparisons of responses to luminance-matched coloured and achromatic patterns show increased activity to the coloured stimuli beginning in area V1 and extending through the new hemifield representation and further anterior in the ventral occipital lobe.

Keywords: colour; retinotopy; visual cortex; cerebral achromatopsia; V4; V8

1. INTRODUCTION

In his insightful review of the neurological literature on cerebral achromatopsia and colour anomia, Meadows (1974) argued that several cortical regions are essential for colour vision. Figure 1, adapted from Meadows' paper, shows three cortical regions he identified: primary visual cortex, a region on the ventral surface and a region on the dorsal surface near the inferior parietal lobule.

Damage to primary visual cortex impairs most forms of conscious vision. For this reason it is not usually counted as a cortical colour specialization. We think, however, that Meadows was correct to list primary visual cortex as an essential component of the colour system. In fact, we think it is useful to go further and remember that colour specialization begins within the retina. The presence of three types of cones, the physiological mechanisms that regulate the gain of the cone signals and the opponent-colours transformations are important elements of colour appearance computations (e.g. Kries 1902; Hunt 1987; Wandell 1995; Fairchild 1998). The spatial structure of the photopic pathways, in which cones dominate the central two degrees of the fovea, is another important colour vision specialization that originates in the retina. This spatial distribution of the cone signals should be considered when we review the role of cortical regions in processing colour signals (Mullen 1991).

The best known portion of Meadows' review was his careful justification of the claim that damage to the ventral surface can interfere with normal colour vision. In this syndrome, called 'cerebral achromatopsia', colour judgements are impaired but other types of visual function (motion, form and depth) are spared. Aware of Semir Zeki's pioneering anatomical and single-unit studies on colour-tuned cells in monkey dorsal V4 ('V4-complex') (Zeki 1983*a*,*b*), Meadows asked whether some part of human ventral cortex might be homologous to monkey V4. Zeki subsequently reviewed the neurological literature on cerebral achromatopsia and used neuroimaging experiments to demonstrate the involvement of human VO cortex in colour perception. While the homology between monkey V4 and human VO cortex is not proved, and many other aspects of the ventral organization remain unclear, the results from many laboratories leave no doubt that Zeki and Meadows are broadly correct: the ventral surfaces of the human occipital and temporal lobes are very active during colour judgements, and damage to these regions can selectively disturb colour vision (Zeki 1990).

There are many unanswered questions about the retinotopic organization and colour signals on the ventral surface of the human brain; we address a few of these

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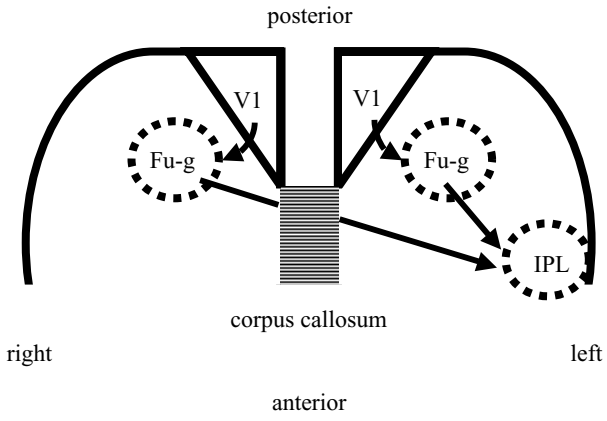

Figure 1. Cortical regions identified by J. C. Meadows as important to human colour perception. The sketch shows an axial view with primary visual cortex (V1) at the occipital pole. The fusiform gyrus (Fu-g) falls on the VO surface and was shown to be associated with cerebral achromatopsia. The inferior parietal lobule (IPL) in the left hemisphere was believed to be important for the relationship between colour, language and imagery.

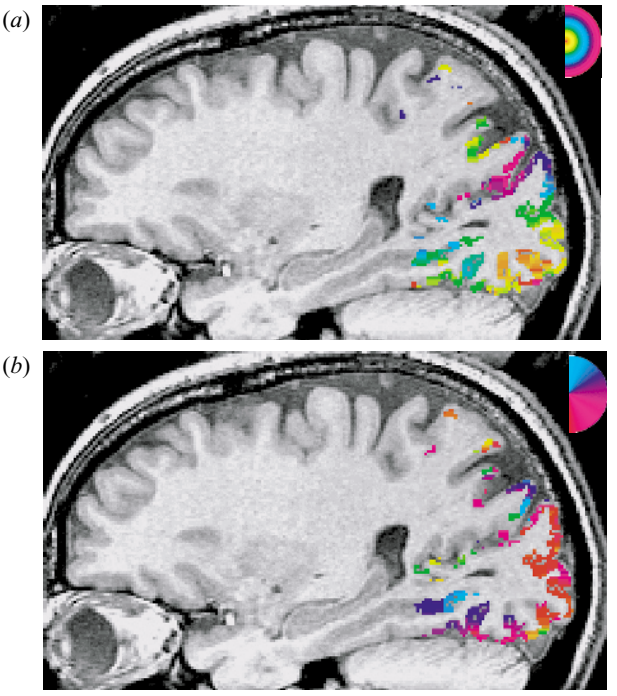

Figure 2. Visual cortex activated by travelling wave stimuli. Only voxels containing neurons with a preferred retinal location will respond to the stimulus. The colour overlay in this sagittal section indicates (*a*) the preferred stimulus eccentricity or (*b*) angle at each voxel within the cortical grey matter. Only locations with a response coherence of more than 0.35 are shown.

questions here. First, in contrast to the widespread assumption that there is very little retinotopy (ordered spatial mapping of the visual field) on the ventral surface, we show that much of ventral cortex is organized retinotopically. Second, we find that adjacent to ventral V3, whose spatial map spans a quarter of the visual field, there is a fourth visual area whose retinotopic map spans an entire hemifield and whose foveal representation is confluent with V1/2/3. This visual field map is not precisely analogous to macaque V4, but because of its position (adjacent to V3v) we refer to the area as 'human V4' or 'hV4'. Third, beyond hV4 there is a large ventral foveal representation that spans approximately half the area of the foveal representation found at the confluence of the early visual areas; it is one of the largest foveal representations in visual cortex. Finally, we compare the VO responses to colour and luminance-matched achromatic stimuli, and we show that responses to coloured stimuli are significantly larger in areas V1, V2, hV4 and other anterior ventral locations.

2. BACKGROUND

Retinotopic organization can be measured in a variety of ways. One simple and useful method is to apply differential imaging (subtractive methodology) and compare responses between two stimuli at different visual field positions. For example, it is possible to identify the boundaries of visual areas V1, V2 and V3 by comparing the responses to targets along the horizontal and vertical meridia (Grill-Spector & Malach 2001). Also, it is possible to obtain a sense of the organization with respect to eccentricity by comparing the responses to foveal and peripheral targets (Levy *et al.* 2001).

If retinotopic organization is the purpose of the study, however, one may wish to extend the differential imaging measurements by studying the responses to targets at more than two positions. Rather than just comparing horizontal and vertical, for example, we might measure the responses to stimuli at a series of angles; and rather than just comparing foveal and peripheral stimuli, we might measure the responses to stimuli at a series of eccentricities. By presenting such stimuli in temporal sequence, one creates a travelling wave of activity in retinotopic cortex (Engel *et al.* 1994, 1997). The signal from each voxel modulates as the stimulus passes through the portion of the visual field that excites the neurons within that voxel; the timing of the peak response measures the visual field position that most effectively excites the neurons in that voxel. These travelling wave methods are also called phase-encoding methods because the phase of the fMRI response measures the most effective stimulus position for each voxel.

We can learn at least two things from the responses to a travelling wave stimulus. First, if the travelling wave stimulus modulates the neural response in a region, then neurons in that region must respond preferentially to stimuli in a localized part of the visual field. By contrast, if the neurons in a region respond uniformly to all spatial positions, there will be no modulation in response to the stimulus. Second, by comparing the responses in adjacent grey matter locations, we learn whether the neurons in a region of cortex form a visual field map. The presence of activity and the orderly arrangement of the visual field preferences are independent sources of information. Naturally, the response amplitudes to the travelling wave stimulus depend on various factors, such as stimulus selectivity of the neurons, spatial resolution of the measurement device and the task demands; these factors must be

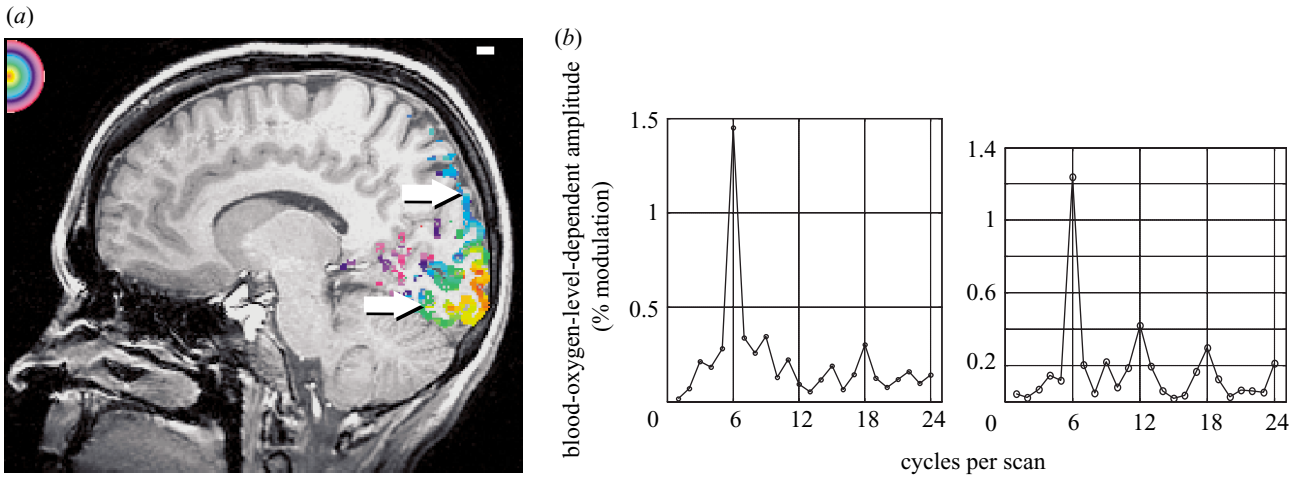

Figure 3. Typical amplitude spectra of the fMRI response to an expanding ring (eccentricity) retinotopic stimulus. There were six stimulus cycles in the scan. The amplitude spectra shown in (*b*) were measured from two regions of interest that are indicated by the white arrows in (*a*). Each region occupies less than 1 cm^2 of cortical surface area. The signals in the anterior portions of the occipital lobe and posterior parietal and all along the ventral surface are substantially above statistical threshold. Other details as in figure 2.

accounted for in interpreting the data. Still, as a first approximation, information about the size of the signal from a travelling wave stimulus measures whether the neurons in a voxel are spatially localized, while the arrangement of the responses between grey matter locations measures whether the cortical region forms a map.

Based on the first round of measurements of retinotopic organization, human visual cortex was divided into retinotopic and non-retinotopic cortex. Several retinotopically organized regions, apparently homologous to macaque areas V1, V2, V3 and V3A, were identified in the early days of fMRI imaging using 1.5T magnetic resonance scanners and relatively simple methods. We now identify and measure these areas routinely (Wandell 1999; Koch *et al.* 2001). A common view is that anterior regions, including parietal and temporal cortex, are not activated by the simple travelling wave stimuli composed of flickering patterns. Instead, it is thought that activity in these regions is elicited only by specialized stimuli associated with the functional specialization of a cortical region; say colour, face and a specific type of object or place (Kanwisher *et al.* 1997; Epstein *et al.* 1999). These anterior regions are called non-retinotopic because in the first round of measurements no clear retinotopic responses were reported.

But the first reports of retinotopic organization are only five years old, and in our view it is too early to draw firm conclusions about the extent of retinotopic and non-retinotopic regimes. With improvements in the quality of the instruments and software tools, the extent of retinotopic cortex is increasing. We have described some advances in our understanding of the organization of dorsal visual cortex in a separate report (Press *et al.* 2001). Here, we focus on colour and the ventral pathways. In offering these results, we caution the reader that even these measurements comprise an incomplete picture of retinotopic organization and that more will be learned. By describing these results, we hope to discuss some new findings and also to forestall any hasty conclusions about the extent of retinotopic organization in human visual cortex.

3. METHODS

The basic experimental methods have been published elsewhere, and we refer the reader to those publications for further details about the general methods (Teo *et al.* 1997; Wandell *et al.* 2000; Press *et al.* 2001). The custom software used to segment grey and white matter and to create flat maps is distributed freely on the Internet. Figure 10 illustrates the spatial relationships between anatomically defined regions in a three-dimensional and flattened cortical view. Several major landmarks are marked in both views. We will make an effort to provide the data and additional custom analysis software upon request.

The fMRI measurements were obtained using a GE 3T scanner and a custom spiral acquisition sequence (Noll *et al.* 1995). The acquisition parameters were set to measure 128×128 sample points in a 260 mm field of view (2 mm $\times$ 2 mm resolution). The plane thickness was set to 3 mm (zero spacing). An entire set of planes was acquired, every time of repetition was 3 s, and a typical set contained 16 planes. The orientation of the planes was coronal and their position was adjusted to cover the occipital lobe and particularly the VO surface. Each stimulus condition was repeated within a scan session between two and four times and the time-series from the different repeats were averaged. There was no spatial filtering of the signals. A linear trend was removed from the time-series at each voxel and response modulations are described as per cent change about the mean signal level at that voxel.

All of the responses shown in the figures are substantially above statistical threshold. This was verified by inspection of the time-series, measuring the response coherence (amplitude at the stimulus fundamental frequency divided by the summed amplitudes of all frequencies), and in some cases by converting the time-series to SPM 99 format and measuring the high statistical reliability of the indicated activations ($p < 0.001$) (Turner *et al.* 1998).

The stimuli were presented on an LCD within a shielded box placed at the foot of the scanner bed. Subjects viewed the display through binoculars so that the effective viewing distance was 0.5 m. The screen extended to 20° in the

periphery. The LCD was calibrated using a spectroradiometer (PhotoResearch PR-650).

Stimuli were created and controlled using custom software based upon the Brainard–Pelli Toolbox (Brainard 1997) and running on a Apple Macintosh G4 (Apple Computers, Inc.) with a 10 bit per gun graphics card (Radius, Inc., Thunder).

The travelling wave stimuli were contrast-reversing black and white patterns that defined either an expanding ring or a rotating wedge. The patterns reversed contrast at 4 Hz and were shown at maximum contrast (*ca.* 90%). The mean screen luminance was 30 cd m^{-2}, and a fixation point was present at all times. Retinotopic organization with respect to the angular dimension was measured using a rotating wedge (angle of 90°). The retinotopic organization with respect to eccentricity was measured using a thin expanding ring (ring width of 2.5°). Both the ring and wedge stimuli had a dartboard structure (radial spatial frequency, 1 cycle deg^{-1}; angular frequency, 12 cycles per 2π). In most of the experiments, the wedges and rings passed through a full display cycle over 36 s, and six cycles were shown in each experimental scan. In some experiments the period was reduced to 24 s and eight cycles were shown.

The colour measurements were patterned after the methods developed by Zeki and his colleagues (McKeefry & Zeki 1997) though there were a few differences. The response differences between colour and achromatic stimuli were measured using a block design. A new pattern was presented every 2 s. Subjects viewed a series of patterns comprised an array of 8×8 rectangular patches spanning 24° of visual angle. During one 12 s block the subject saw a series of six random checkerboard patterns. All the patterns in each block were either pure-luminance varying or full chromatic stimuli. This stimulus is illustrated in figure 11.

The colour properties of the display were specified using a simple opponent-colours scheme of luminance (L + M), S-cone, and red-green opponent signals (L − M). In one block the patterns had only an achromatic (intensity scaling) contrast difference from the neutral background. In this condition, L + M and S-cone contrast were set at equal and L − M contrast was set to zero. The luminance and S-cone contrast difference between the background and each patch was randomly and uniformly selected from within the available contrast range ±17%. In the second 12 s block the L + M contrasts matched the values in the first block; the S-cone and L − M contrasts were randomly selected from the L − M (max ± 6%) and S (max ± 17%) directions.

During the task, subjects were required to detect the orientation of a superimposed 'C' shape. The shape was created by adding a small amount of L + M signal to seven of the rectangles. The additional mean signal was very slight, and it was adjusted so that subjects scored about 80% correctly in identifying the orientation of the target. In this way, we hoped to eliminate attentional modulations that might arise because of the stimulus differences.

4. VO CORTEX: RETINOTOPY

(a) *VO cortex responds to travelling wave stimuli*

How much of visually responsive cortex is retinotopically organized? Using travelling wave stimuli, we consistently find responses that extend well onto the lateral and ventral surfaces of the occipital lobe and often into parietal and temporal cortex.

Figure 2 shows a region of cortex that responds reliably to a travelling wave stimulus (expanding ring). The stimulus was a flickering contrast pattern contained within an expanding ring (figure 2*a*) or a rotating wedge (figure 2*b*). The colour overlay indicates the principal visual field eccentricity represented at each grey matter location. The expanding ring stimulus evokes activity extending from the occipital pole far forward into parietal and temporal cortex. Note the continuous band of activity along the ventral surface of the brain in regions that have been labelled as selectively responsive to various special categories, such as faces, objects and colours.

The data shown in figure 3 are a second typical example of the travelling wave measurements (expanding ring) we obtain routinely from individual observers on a 3T magnet using our current methods. In both figures 2 and 3, the activity is plotted conservatively in that only very reliable signals (coherence greater than 0.35) are shown. The amplitudes of the harmonic components of the time-series in several cortical locations are shown in figure 3*b*. Each of the selected regions of interest spans an area of *ca.* 6 mm × 6 mm within the grey matter. The reliability of the signal can be judged by comparing the amplitude at the fundamental frequency of the travelling wave with the amplitude at nearby frequencies. In all cases the amplitude at the fundamental frequency of the stimulus (six cycles per scan) is many standard deviations from the mean amplitude of the nearby temporal frequencies.

In measurements using the 3T system, travelling wave stimuli routinely activate regions from the occipital pole well into the VO lobe and dorsally past the parietal–occipital sulcus. We see this activation using a simple achromatic flickering contrast pattern, not an object or a face or a colourful design. As we reviewed in § 2, the presence of strong activity in response to a travelling wave stimulus shows that there is a preference for one portion of the visual field compared with another. Note that the responses on the ventral surface are comparable in magnitude and estimated foveal position with those in V1, further suggesting that the degree of spatial selectivity is similar. We have made additional measurements in six other individuals and found consistent results.

(b) *VO cortex includes a lower visual field representation*

A response to phase encoded retinotopic stimuli demonstrates a spatial preference within individual voxels but the presence of a response does not demonstrate that there is an organized map on the cortical surface. To detect the presence of a visual field map we must visualize how these spatial preferences are distributed on the grey matter surface. To visualize the spatial pattern, it is convenient to display the data either on three-dimensional renderings of the brain or on 'flat maps': computationally flattened representations of the cortical surface.

Figure 4 contains examples of the visual field maps of angle and eccentricity in two representative subjects. The colour overlay, which codes the visual field map, is superimposed upon a greyscale representation of the underlying anatomy. Light greyscale shading represents a gyrus and dark shading represents a sulcus (the flat map is further described in § 3). In figure 4*a*,*c* the colour overlays measure the preferred angular direction. The locations of V1, the motion complex (V5) and the ventral surface are denoted on the flat maps. There are several differences in

the responses from these two subjects, but there are also several important similarities. The similarities we describe here have also been observed in four other subjects.

First, consider the angular measurements in figure 4*a*,*c*. Notice that the ventral surface contains a substantial lower-field representation (occupying the magenta region of the colour map). A white arrow denotes the location of one large lower-field representation in roughly corresponding locations for the two observers. At the resolution we have produced this figure, it is difficult to appreciate the precise position of this representation. In more detailed analyses of the white-circled region presented below, we find that this representation abuts the ventral V3 representation. We see this feature in all observers. Second, notice that there is an upper field (cyan) representation on the dorsal surface. A black arrow denotes the location of this representation in each of the observers. Hence, both the ventral and dorsal surfaces contain a full representation of the hemifield.

(c) *VO cortex includes a very large foveal representation*

The colour overlays in figure 4*b*,*d* show those cortical regions with a preferred response within the central 20° of the visual field. The largest set of foveal representations falls at the confluence of areas V1, V2, V3 and extends from the most posterior aspect of the calcarine sulcus onto the lateral surface of the brain. The width of this set of foveal representations is close to 4.5 cm in both observers and covers a total area of between 16 and 20 cm^2. There is a second distinct and large foveal representation that can be plainly seen in all observers. This second foveal representation falls on the ventral surface and spans a width of *ca*. 2.5 cm and an area of *ca*. 6–10 cm^2. Notice that the preferred spatial location in this ventral foveal representation is very similar to the preferred locations in the large representation at the confluence of the early visual areas.

There are several other foveal representations visible in figure 4. First, notice the foveal representation in the motion-selective region of cortex. This foveal representation falls within motion-selective cortex located on the lateral margin of the occipital lobe, near the temporal–parietal–occipital junction. Yet another displaced foveal representation can be seen on the dorsal surface within area V3A. We have commented on this representation and also another one that falls further anterior in area V7. We generally find that the preferred eccentricity in motion selective cortex is slightly more peripheral than the preferred eccentricities in early visual areas or on the ventral surface. This could arise for several reasons, though we suspect the difference is due to the presence of neurons with larger receptive fields in V3A/B and motion-selective cortex (Tootell *et al.* 1997; Smith *et al.* 1998; Press *et al.* 2001).

The eccentricity map on the ventral surface is shown once more in figure 5. In this case, rather than using a flat map we show the preferred stimulus location on a three-dimensional rendering of the boundary between the white and grey matter of the brain.

These measurements were obtained from the posterior one-third of the brain, extending into posterior parietal and temporal cortex. The data are shown for a third subject, A.W., and also from subject B.W. whose data are shown in previous figures. Figure 5*a* shows a medial-ventral view of the brain. From this view, one can see the classic eccentricity map extending along the calcarine sulcus but extending well into dorsal and ventral cortex. Figure 5*b* shows the time-series of the fMRI responses measured from the foveal representations on the ventral surface. These large signals show the clear preference for foveal activation in a large ventral region. The nearby area is also organized into a map of the visual field.

(d) *hV4*

The importance of VO cortex for colour perception in humans was clearly established by Meadows' and Zeki's reviews of lesion data (Meadows 1974; Zeki 1990) and more recently by neuroimaging experiments using positron emission tomography and fMRI (Zeki *et al.* 1991; McKeefry & Zeki 1997; Hadjikhani *et al.* 1998; Bartels & Zeki 2000). In the neuroimaging experiments, Zeki *et al.* (1991) found a preferential response to colour compared with luminance-matched achromatic stimuli on the ventral surface and they labelled this spot hV4. McKeefry and Zeki further reported that responses to colour stimuli 2.8–10° above fixation were located adjacent to responses to stimuli placed 2.8–10° below fixation, both on the ventral surface. This showed a hemifield representation on the ventral surface: a result that is consistent with hemiachromatopsia reports in the neurological literature (McKeefry & Zeki 1997).

Hadjikhani *et al.* (1998) subsequently confirmed a VO colour responsive region with a hemifield map representation. They argued that this hemifield representation could not be V4, but rather it must be a new colour area they called V8. The new area is based upon a definition of V4v as a quarter field representation adjacent to V3v. They proposed that V8 is adjacent to V4v, contains a hemifield map, a distinct fovea, and that its angular representation is perpendicular to the V4v representation. This claim has met some resistance from Zeki and his colleagues (Bartels & Zeki 1998, 2000; Zeki 2001).

We find that the visual map adjacent to V3v represents the entire contralateral hemifield, not a quarter field as proposed by Hadjikhani *et al.* (1998). This map occupies *ca*. 4 cm^2 of cortex and includes a foveal representation that is confluent with that of areas V1/2/3. The homology of this area to macaque V4 is uncertain because the human map does not extend onto the dorsal surface nor does it surround V1. However, due to its location adjacent to V3v, we propose calling this hemifield representation hV4. We agree with Hadjikhani *et al.* that there is a separate and distinct foveal representation present on the ventral surface beyond hV4. This foveal representation is located 3–5 cm from the confluent V1/2/3 foveal representation and it is larger than the foveal representation in V1. In addition to this distinct fovea, there is clearly considerable retinotopic organization beyond hV4. We do not yet have adequate power in our measurements and analysis tools to confidently label these regions into functional visual areas, although this should prove possible in the future.

The justification for our proposed organization is presented in figures 6 and 7. The coloured images in these figures show travelling wave measurements of angular and

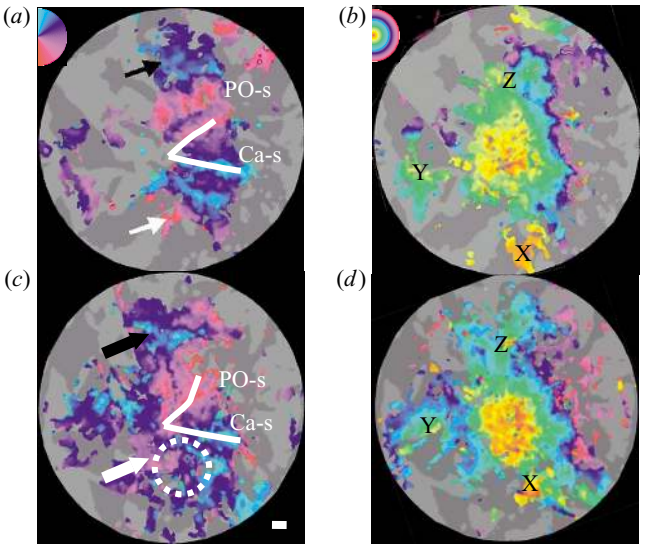

Figure 4. Angular and eccentricity maps for two subjects shown on flattened representations of the left occipital lobe. The flat maps are centred near the occipital pole and have an 8 cm radius (scale bar, 1 cm). Shading indicates a sulcus (dark) or gyrus (light). Dorsal and ventral are up and down; lateral and medial are left and right. The flat maps are further described in § 3. (*a*,*c*) Measurements of angular retinotopy. The calcarine sulcus (Ca-s) and parietal–occipital sulcus (PO-s) are marked. The inset shows the preferred angular direction, ranging from cyan (upper) to blue (horizontal) to red (lower). The white line denotes the V1 hemifield representation that falls within the Ca-s. The black arrows indicate positions on the dorsal surface that respond well to the upper visual field, and the white arrows indicate positions on the ventral surface that respond well to the lower visual field. The dashed white circle indicates the region on the ventral surface that is analysed in more detail in subsequent figures. (*b*,*d*) Measurements of eccentric retinotopy for the same two observers. The preferred eccentricity between 0 and 20° is indicated by the colour overlay, with red/yellow representing the central 5°, green/cyan representing 5–10°, and blue/magenta representing 10–20°. The large red/yellow region near the occipital pole falls at the confluence of V1/2/3. The second large foveal representation (marked 'X') on the ventral surface is analysed in subsequent figures. The foveal representation on the lateral surface (marked 'Y') falls within motion-selective cortex. The foveal representations on the dorsal surface (marked 'Z') have been described elsewhere (Press *et al.* 2001). In all maps, the preferred visual field location is indicated only at cortical positions with a signal coherence of at least 0.35.

eccentric representations. The images code measurements from a 7 cm diameter region within VO cortex. The images appear blurred because these measurements are made at the current resolution limit of our instruments: there are approximately five sample points per centimetre, and the spatial blurring of the signal by the vasculature extends over several millimetres (Engel *et al.* 1997). While we use the pseudo-colour images to guide our interpretation of the spatial organization and to suggest hypotheses, our conclusions are based on the graphs and quantitative analyses presented along with these images.

The images in these figures show travelling wave measurements from two observers; the same pattern has been observed in every other observer we have measured. Angular and eccentricity measurements are shown at the top and bottom. Because no significant differences were found between the right and left hemispheres, all of the angular colour maps and positions have been adjusted to a 'left hemisphere' format where angular retinotopies are plotted in a magenta/blue/cyan pseudo-colour map and eccentricity retinotopies have a red/yellow/green map.

First, consider the angular measurements shown in figure 6*a*. The large cyan colour band represents the upper visual field and defines one boundary of V3v. Beyond this boundary the preferred angular representation continues through blue (horizontal) and then onto magenta and red (lower vertical). The data indicate a continuous progression of preferred orientations that define a full hemifield representation, with the upper visual field represented medially and the lower visual field represented laterally.

We note that this arrangement is similar to that described by McKeefry & Zeki (1997). The green circles in figure 6*b* measure the fMRI signal phase across this band between the two black circles in figure 6*a*. The phases span 3 rad, substantially more than what would be expected if V4v were restricted to a quarter field representation.

Furthermore, by considering the image in figure 6*d*, we find a consistent eccentricity map as well. There is a foveal preference (orange, yellow) that merges with the foveal representation of V3v and (not shown) V1/2. This preferred eccentricity map is orthogonal to the preferred angular map, so that this region contains a full hemifield with respect to both visual field dimensions.

The orthogonality of the two representations can be demonstrated by plotting the signal phase for the eccentricity measurements across the same path that we used to plot the angular phase. The plot marked with green circles in figure 6*e* shows that the phases of the eccentricity measurements are close to constant, while the angular measurements shown in the upper graph span the entire hemifield with phases from *ca.* 0 to π rad.

The hemifield map spans *ca.* 2 cm on each side. This is approximately twice the width of the quarter field maps in V2 and V3. The location of this hemifield representation is indicated on the images in figure 6*a*,*c*,*d*,*f* by the dashed polygon and the label 'hV4'.

The spatial organization of the eccentricity map is very systematic in four subjects (eight hemispheres) where we have focused on the ventral surface. The typical pattern is shown in more detail in figure 7. Beginning in the hV4 fovea, we can trace a path to the second foveal representation. For 2 cm along this path, the eccentricity preference becomes increasingly eccentric. Then near the 10° representation (green colour code) the eccentricity map reverses and the response preference returns back towards the fovea.

This progression of preferred eccentricities can be seen in the colour images, but it is particularly clear in the measured time-series shown on the right of figure 7. The graphs show the travelling wave signal measured at each of the circled grey regions of interest. In all observers and all hemispheres, the retinotopic map varies reliably from fovea to periphery and then back. We found no way to reconcile these measurements with the proposed quarter

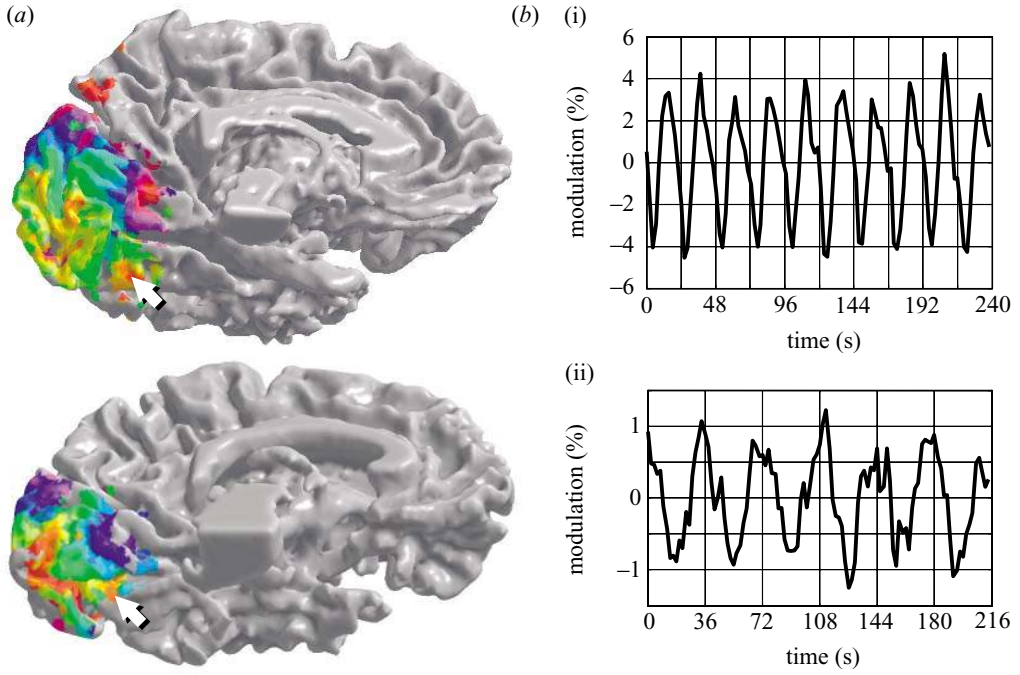

Figure 5. (*a*) Three-dimensional renderings of the eccentricity map seen from a medial/ventral view. (i) Data from a third subject A.W.; (ii) data from subject B.W. (*b*) The time-series of the activity from the ventral foveal representation, indicated by the arrow. The experiments used different numbers of cycles and different duty cycles. In both cases, the time-series is well above statistical threshold. Other details as in figure 2.

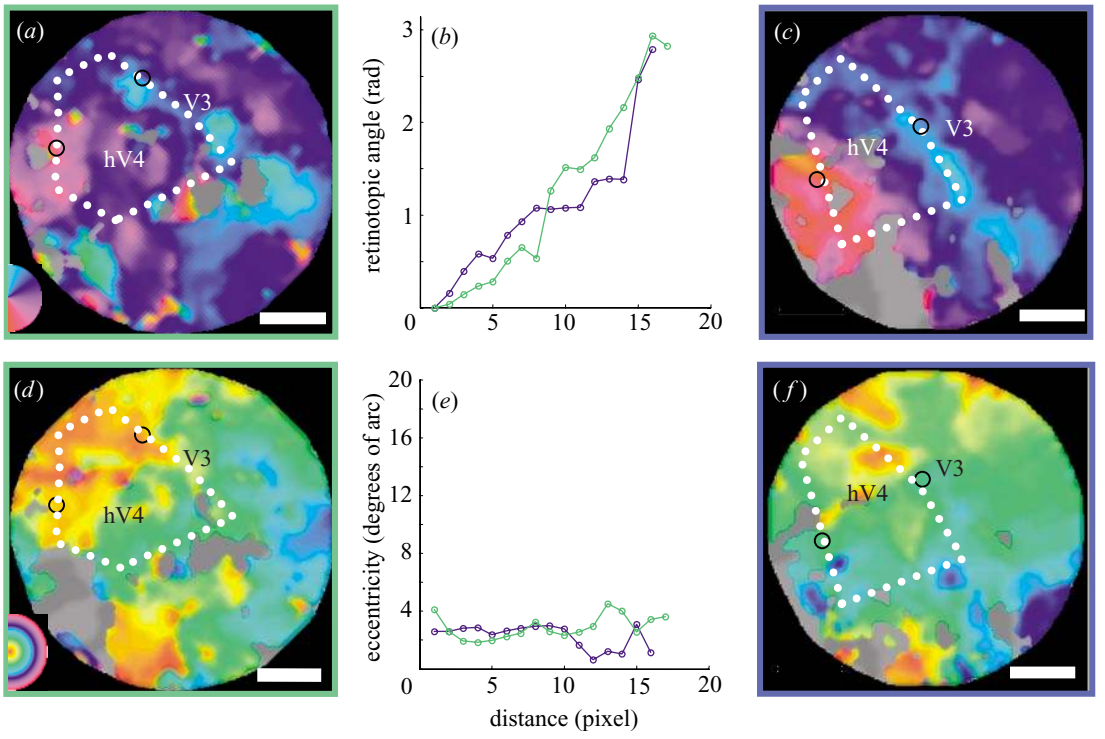

Figure 6. Retinotopic organization in VO for two subjects. The images show angular (top) and eccentricity (bottom) maps; the left and right images are from two subjects (A.B. and B.W.). In the angular maps (*a*,*c*), cyan represents the upper vertical meridian, blue/magenta the horizontal and red the lower vertical meridian. The hemifield representation of hV4 is indicated by the dotted white polygon, and the general location of ventral V3 is shown. The eccentricity maps (*d*,*f*) from foveal (red/yellow) to peripheral (green and cyan) run perpendicular to the angular map. The graphs (*b*,*e*) show the measured angular (*b*) and eccentricity (*e*) values on a path between the black circles marked on the hV4 boundary. Data from subject A.B. are plotted in blue, data from subject B.W. are plotted in green. Along these paths the angular phase measurements span 3 rad (*b*), indicating a hemifield representation while the eccentricity measurements are approximately constant (*e*). The VO foveal representation falls at the bottoms of the maps in (*d*) and (*f*). The expanding ring stimulus extended to a 20° radius (blue/magenta), but the preferred eccentricities in hV4 were more central (cyan/blue). Scale bar, 1 cm.

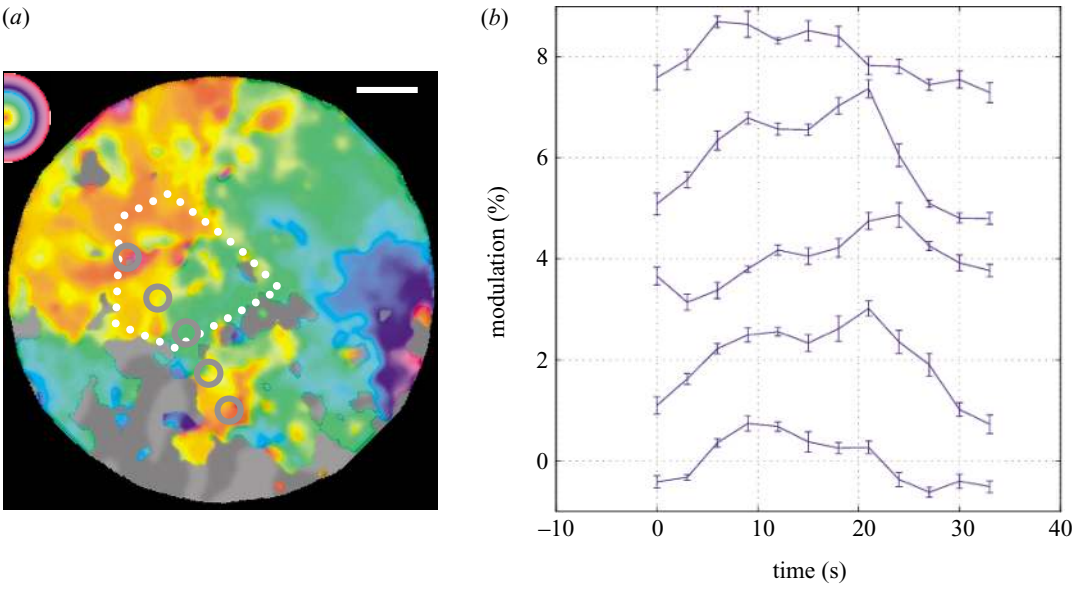

Figure 7. The eccentricity map in ventral cortex near hV4. (*a*) The two prominent red/yellow regions represent the fovea at the confluence of V1/2/3/4 (upper left) and the displaced foveal representation on the ventral surface (bottom middle). The peripheral signals (blue) fall within areas V2/3. Area hV4 is denoted by the dashed white polygon. The grey circles indicate a series of regions of interest that fall between the two large foveal representations. (*b*) The average fMRI time-series during a single stimulus cycle from each region of interest on the left. The signal amplitudes are quite significant and reliable, representing about 1% modulation about the mean. The individual curves are displaced vertically for clarity; their order corresponds to the ordering of the regions of interest. The middle curve measures the time-course at the peripheral boundary of hV4. The phase of the curves varies systematically and reverses direction at this boundary. Colour overlays are included only at locations with a coherence of at least 0.35. Scale bar, 1 cm.

field V4v and hemifield V8. In every case we could identify hV4 as a simple map of the entire contralateral hemifield.

A brief examination of the images shows that there are additional retinotopic maps beyond hV4. But a definitive assessment of how this region of VO is organized should await further improvements in the data and analysis tools.

(e) *VO cortex: colour*

Finally, we consider the relationship between the travelling wave measurements and the signals evoked by a colour experiment. We have compared the signals evoked by alternating coloured and luminance-matched achromatic patterns (see figure 11), and we can confirm the general observations described in the more recent observations from Bartels & Zeki (1998, 2000) and Hadjikhani *et al.* (1998). The regions that respond preferentially to the colour stimulus begin in area V1 and continue along the ventral pathway into VO.

Figure 8 indicates the general position of the strongest colour activations in three observers. In all three subjects we find significant activity in V1, V2, hV4 and nearby VO regions. By comparison, there is very little preference for the coloured stimuli in dorsal regions or in ventral V3. For one of our observers (though not all) there was also a stronger response to the *achromatic* stimuli on the dorsal surface.

Figure 9 shows the spatial distribution of activity on the VO surface in both hemispheres of three subjects. There is very significant activation in synchrony with the colour stimulus in hV4 and the surrounding region. Only the locations with a very high activity ($p < 0.001$) are shown; if we marked every point that was active at some modest significance level (e.g. $p < 0.02$), most of this region

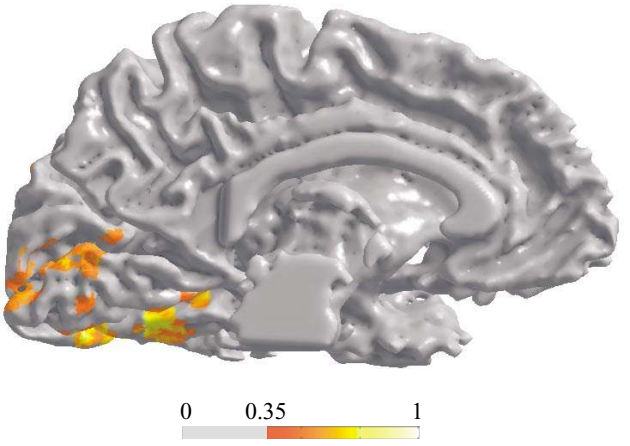

Figure 8. Mid-sagittal view of colour exchange activations. Activations exceeding a coherence level of 0.4, approximately equivalent to a statistical threshold of $p < 0.001$, are shown. There is significant activation in the calcarine sulcus as well as along the ventral surface. Subject A.W.

would show activity. The most powerful responses are not constrained to the central foveal regions; though recall that the entire region appears to prefer signals within the central 10°. Hence, we do not think the punctate nature of the activation pattern is meaningful.

To facilitate comparisons between groups and experiments, we chose an experimental design that was similar that used by the London group (McKeefry & Zeki 1997). In this design, observers are not asked to fixate, which means that the effective stimulus visual field position is not controlled. Given that we now know that VO is retinotopically organized, we suspect that some of the differ-

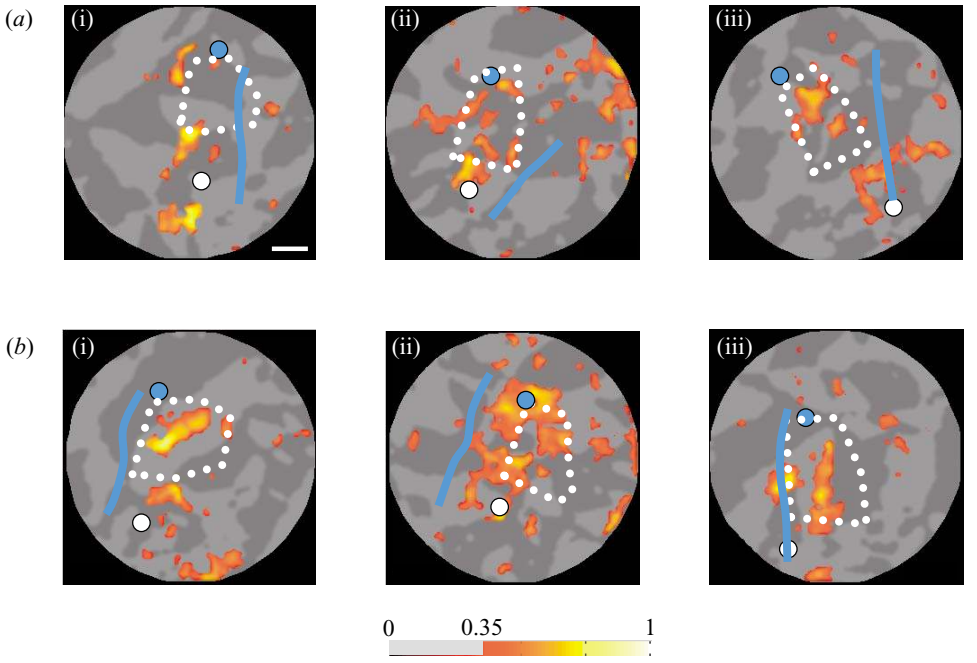

Figure 9. Locations responding preferentially to chromatic compared with achromatic stimuli in three subjects. Data are shown for three subjects ((i) A.W., (ii) A.B., (iii) B.W.). (*a*) Left hemisphere; (*b*) right hemisphere. The hV4 boundary is marked by the dotted white polygon, and the collateral sulcus is marked in blue. The foveal representations in hV4 (blue dot) and VO (white dot) are marked. The unfold spans 7 cm. Only locations with response coherence greater than 0.35 are shown. Scale bar, 1 cm.

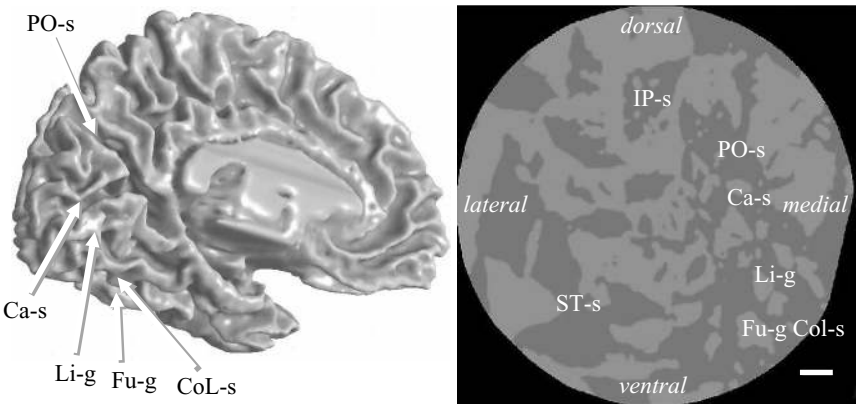

Figure 10. The relationship between the flattened and folded brains. The flattened representations used in previous figures are organized so that the calcarine sulcus falls near the horizontal axis. Dark regions show sulci and light regions show gyri. Dorsal and ventral are up and down, respectively. Landmarks indicated on the flat map are as follows: IP-s, intraparietal sulcus; Ca-s, calcarine sulcus; Li-g, lingual gyrus; Fu-g, fusiform gyrus; ST-s, superior temporal sulcus; PO-s, parietal–occipital sulcus; CoL-s, collateral sulcus. Scale bar, 1 cm.

ences between subjects may be caused by differences in eye movement patterns or differences in individual strategy when performing the target detection task. The experimental design choices can be modified in future studies, allowing a more precise measurement of the colour responses in VO.

5. SUMMARY

We summarize our observations with three major points. First, a considerable amount of occipital cortex responds well to the travelling wave stimulus. This demonstrates that most of occipital cortex is stimulated preferentially by a restricted spatial region of the visual field. Further, these spatial preferences are generally organized into retinotopic maps. The secure identification of these maps should await additional data and improvements in the analytical tools (Koch *et al.* 2001).

Next, because of the debate in the literature, we have made a particular effort to understand the region near putative V8 (Hadjikhani *et al.* 1998; Bartels & Zeki 2000; Zeki 2001). We find a hemifield map adjacent to V3v. While we see a visual field map that is generally consistent

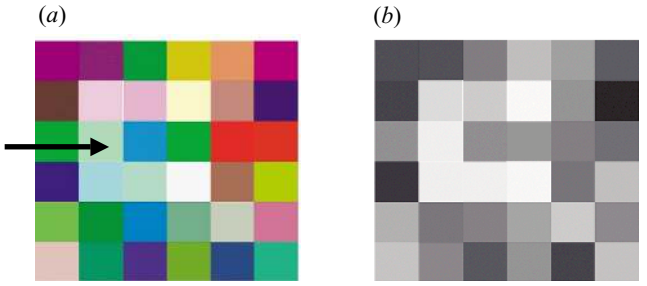

Figure 11. A pair of luminance-matched stimuli used in the Mondrian colour-exchange experiments. A random draw of the pattern is shown every 2 s. For 12 s blocks the pattern is coloured (*a*) and for 12 s blocks the pattern is achromatic (*b*). To control for attention, subjects are asked to identify the orientation of the opening in the 'C' throughout the experimental scan (10 blocks). The arrow indicates the location of the C, but the arrow is not present during the experiment.

with the reports that led to V8, we cannot reconcile the details of the angular and eccentric maps in such a way that V8 represents a hemifield adjacent to a V4v quarter field. Rather, we think that in the human, the fourth visual area represents the central 10° of the entire hemifield. We note that the presence of a ventral area adjacent to V3v that represents an entire hemifield extends a trend that can be found in macaque. In that animal, the ventral representation of V4 includes a substantial portion of the visual field that lies below the horizontal midline (Gattass *et al.* 1988). We propose referring to this hemifield map as hV4.

Finally, we examined the spatial distribution of colour activations on the ventral surface. To coordinate our measurements with earlier investigators, we used a colour-exchange protocol in which eye movements are uncontrolled and colour selections are randomized. Using this protocol, we do find colour activation beginning in V1 and extending onto the ventral surface. We do not find a distinctive and highly localized pattern that is consistent across observers. We expect that by using better-controlled colour test stimuli (for example, stimuli that selectively excite individual cone classes or opponent colour pathways), we will be able to learn more about the colour signals within the ventral pathways.

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GLOSSARY

fMRI: functional magnetic resonance imaging
hV4: human V4
LCD: liquid crystal display
VO: ventral occipital