Color responsiveness argues against a dorsal component of human V4

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The retinotopic organization, position, and functional responsiveness of some early visual cortical areas in human and non-human primates are consistent with their being homologous structures. The organization of other areas remains controversial. A critical debate concerns the potential human homologue of macaque area V4, an area very responsive to colored images: specifically, whether human V4 is divided between ventral and dorsal components, as in the macaque, or whether human V4 is confined to one ventral area. We used fMRI to define these areas retinotopically in human and to test the impact of image color on their responsivity. We found a robust preference for full-color movie segments over a luminance-matched achromatic version in ventral V4 but little or no preference in the vicinity of the putative dorsal counterpart. Contrary to previous reports that visual field coverage in the ventral part of V4 is deficient without the dorsal part, we found that coverage in ventral V4 extended to the lower vertical meridian, including the entire contralateral hemifield. Together these results provide evidence against a dorsal component of human V4. Instead, they are consistent with human V4 being a single, ventral region that is sensitive to the chromatic components of images.

Keywords: color vision, retinotopic mapping, functional imaging, visual cortex, homology

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Introduction

Much of our current understanding of the human visual system has its foundation in animal models, but more recently functional MRI has facilitated comparison of visual processing in humans and non-human primates. One area of comparison is the retinotopic organization of early visual cortex. On the whole, there is close homology between humans and non-human primates in the organization of their visual areas (Sereno et al., 1995), but one point of suggested difference is in area V4. Unlike macaque, where V4 is split into ventral and dorsal components that together represent a hemifield, in humans it is most commonly reported that V4 has an unbroken ventral hemifield representation, without a dorsal component (Brewer, Liu, Wade, & Wandell, 2005; Larsson & Heeger, 2006). An alternative view is presented by Hansen, Kay, and Gallant (2007), who argue that current evidence for the ventral hemifield model of human V4 is not sufficiently strong to reject a model homologous to the organization found in macaque.

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Organization of V4 in non-human primates

The retinotopic organization of visual areas in non-human primates has been investigated primarily by mapping visual field coverage using functional and anatomical connections between visual areas (Felleman & van Essen, 1991), although more recently fMRI methods have also been applied (Brewer, Press, Logothetis, & Wandell, 2002; Fize et al., 2003). In macaque, the location and visual field representation of areas V1, V2, and MT are the most clearly defined (Felleman & van Essen, 1991; Lyon & Kaas, 2002; Rosa & Tweedale, 2005; van Essen & Zeki, 1978). Adjoining V2, area V3 is most likely another hemifield representation, mirror reversed to V2 (Brewer et al., 2002; Fize et al., 2003; Lyon & Kaas, 2002), although it has previously been proposed that the ventral and dorsal parts may be separate areas (referred to as VP and V3, respectively), and that the dorsal part may represent an entire visual hemifield (area DM, see Lyon & Kaas, 2002, for summary).

Partly due to uncertainty of its borders with V3, and also due to the larger receptive field size of neurons there (for example, van Essen & Zeki, 1978), the definition of area V4 is disputed. Currently, area V4 in macaque is usually defined as a split hemifield representation, made up of dorsal and ventral quarterfields, in a similar manner to areas V2 and V3. The main uncertainty concerns the anterior borders of V4 (Fize et al., 2003). The quarterfields of V4v and V4d share a border with V3 at a vertical meridian representation, but it is unclear whether the anterior border of V4d reaches a horizontal meridian or whether the dorsal component of V4 represents just under a quarterfield. According to the first view (Brewer et al., 2002; Pigarev, Nothdurft, & Kastner, 2002), both V4v and V4d represent a quarterfield, while according to the second view (Fize et al., 2003; Gattass, Sousa, & Gross, 1988), V4d does not represent the horizontal meridian and V4v represents the remainder of the visual field, including the upper quarterfield and slightly below the horizontal meridian.

In an fMRI study, Brewer et al. (2002) used traveling wave stimuli, standard for mapping retinotopy in humans, to investigate the organization of visual areas in macaque. In agreement with the electrophysiological work, they report that V4 is a split hemifield with ventral and dorsal quarterfields. They also quantitatively analyzed the visual field coverage and found an asymmetry in the eccentricity maps of V4: the central visual field falls more in the ventral than the dorsal region.

Soon after its identification, area V4 was reported to have a strong preference for color (van Essen & Zeki, 1978; Zeki, 1973), which led to the suggestion that area V4 may be a "color center" in early visual cortex. Others have argued against this idea (Lennie, 1999), citing evidence that the spectral sensitivity of V4 cells is no narrower than that of earlier areas (de Monasterio & Schein, 1982; Desimone, Schein, Moran, & Ungerleider, 1985). However, it may be that V4 is not specialized for discriminating different wavelengths of light (Heywood, Gaffan, & Cowey, 1995) but is involved in higher order processing of chromatic information (Schiller & Logothetis, 1990; Walsh, Carden, Butler, & Kulikowski, 1993; Walsh, Kulikowski, Butler, & Carden, 1992) or color constancy (Kusunoki, Moutoussis, & Zeki, 2006; Wild, Butler, Carden, & Kulikowski, 1985).

Controversy over the organization of human V4

The functional role and location of human area V4 remains controversial. Following reports of strong color responses in rhesus monkey visual cortex (Zeki, 1973), earlier reports of specific deficits in color vision following cortical lesions were reinterpreted as potential evidence for a color processing area in human visual cortex (for a review, see Zeki, 1990). In normal human cortex, a possible homologue of macaque V4 was first reported by Lueck et al. (1989) and later by Zeki et al. (1991), who used PET to show a color responsive area in the region of the lingual and fusiform gyri.

With the advent of high-resolution fMRI, our understanding of retinotopic map organization in human visual cortex has advanced considerably (for a review, see Wandell, Dumoulin, & Brewer, 2007). Early studies (DeYoe et al., 1996; Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; Sereno et al., 1995; Tootell et al., 1997) found visual field maps, each with full hemifield representation, that were consistent with human V1, V2, and V3 of the same organization as found in macaque. However, when looking for the human homologue of macaque V4, these early studies found only a ventral quadrant representation, without a clear dorsal counterpart (see earlier review by Wandell, 1999). The ambiguity of the area corresponding to V4d in macaques was due in part to early inconsistencies in the definition of human V3A, an area that in macaque adjoins V3d along with V4d. Wandell, Brewer, and Dougherty (2005) summarize the confusion within the early literature on V3A and neighboring areas V3B and V7, noting that the small size of these areas and the generally weaker fMRI signals in the intraparietal region contributed to the inconsistent reports of their retinotopic organization.

McKeefry and Zeki (1997) reported a color-sensitive region in ventral human visual cortex, without a dorsal component, which they labeled V4. Although they did not use retinotopic mapping, they showed that this region responds to both the superior and inferior parts of the visual field and suggested that an entire visual hemifield may be represented ventrally in human V4. Later studies using retinotopic mapping supported this claim: Wade, Brewer, Rieger, and Wandell (2002) found a hemifield representation in ventral V4, which they labeled "hV4" (human V4) to disambiguate it from V4 as defined in macaque. In recent years, many studies have used retinotopic mapping to define hV4 as a ventral hemifield representation (Arcaro,

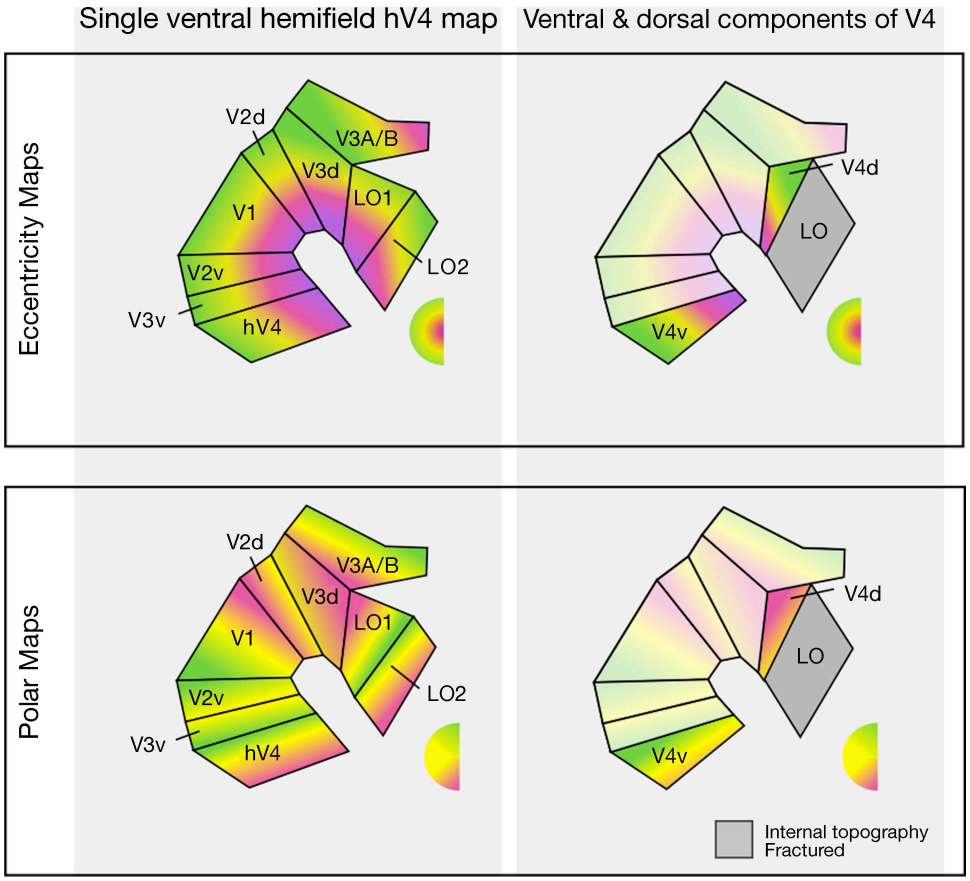

Figure 1. Two alternate models of human V4. In each of the four panels, the schematic shows the predicted visual field preference across a flattened map of the right hemisphere of the visual cortex. The upper maps are colored according to eccentricity preference and the lower maps show polar preference, with the semicircular key to the lower right indicating the part of the visual field corresponding to each color. The model on the left, with a single ventral hemifield hV4 map, is derived from the definitions of Brewer et al. (2005) and Larsson and Heeger (2006). The model on the right, where V4 is split into ventral and dorsal components, is based on the definitions in Hansen et al. (2007). Those areas that are common to both models have been whited out and are not labeled on the right-hand side to highlight the points of difference between the models.

McMains, Singer, & Kastner, 2009; Brewer et al., 2005; Larsson & Heeger, 2006; Wandell et al., 2005), although coverage of the lower vertical meridian in hV4 is typically less clear than in V1–V3 (Larsson & Heeger, 2006; Tyler et al., 2005).

An alternative scheme for the organization of V4 in humans is that the lower vertical meridian and nearby angles are represented by a dorsal component of V4. Most recently, Hansen et al. (2007) suggested the V4d model as providing quantitatively better descriptions of visual field coverage than the hV4 model (but see Winawer, Horiguchi, Sayres, Amano, & Wandell, 2010, for an account of how fMRI studies tend to underestimate the visual field coverage of ventral V4). Their model has a ventral V4, which represents slightly more than a quadrant of the visual field, and a dorsal V4, abutting V3d, which represents the lower vertical meridian and nearby angles. Unlike Larsson and Heeger (2006), who argued for the existence of two lateral occipital areas, each with a hemifield representation, Hansen et al. (2007) reported the existence of a single lateral occipital region beyond V4d with no clear retinotopy. The two alternate models of human V4 and LO are illustrated schematically in Figure 1.

Color responsivity of human V4 and ventral occipital cortex

As with non-human primates, in humans there have been varying reports of whether V4 shows a preference for colored stimuli and whether there is a "color center" in human visual cortex. Lesion studies suggest the particular involvement of ventral areas in processing color. Lesions to ventral parts of the occipital cortex can result in cortical color blindness (achromatopsia) or various color vision deficits (dyschromatopsias; Beauchamp, Haxby, Rosen, & DeYoe, 2000; Bouvier & Engel, 2006; Damasio, Yamada, Damasio, Corbett, & McKee, 1980; Gallant, Shoup, & Mazer, 2000; Meadows, 1974; Zeki, 1990).

Early fMRI studies (without retinotopic mapping of visual areas), while searching for a human color center, reported a strong color preference in ventral areas that

most likely include ventral V4 and a more anterior area labeled V4α (Bartels & Zeki, 2000; Beauchamp, Haxby, Jennings, & DeYoe, 1999). Hadjikhani et al. (1998) and Tootell and Hadjikhani (2001) report that V8 but not V4 responds to color afterimages, although the area they label V8 would be included in V4 (at least in part) according to the ventral hemifield model of V4. In a classifier study on the binding of motion and color, Seymour, Clifford, Logothetis, and Bartels (2009) report that while classifiers trained on data from V1, V2, V3, V3A, and MT+ were biased toward learning the motion rather than the color of the stimulus, when trained on data from V4 the classifiers showed a weaker bias for learning color rather than motion.

Another area suggested to be a "color center" in humans is area VO, which is located adjacent to V3v and V4v with a separate foveal representation, and shows a strong response to colored stimuli (Brewer et al., 2005; Liu & Wandell, 2005; Mullen, Dumoulin, McMahon, de Zubicaray, & Hess, 2007; Wade et al., 2002). Mullen et al. (2007) report that VO but not V4 shows an overall preference for isoluminant colors over luminance-defined stimuli with the same cone contrast. Liu and Wandell (2005) compared V1 and VO in their response to color and other stimulus features and showed that while V1 and VO both respond to color, VO, but not V1, has a temporal frequency tuning similar to color perception. Jiang, Zhou, and He (2007) also reported that VO but not earlier areas showed responsiveness that correlated with perceptual experience when subjects viewed chromatic flicker.

Anterior to V4 and VO, in a region that possibly corresponds to V4α, Murphey, Yoshor, and Beauchamp (2008) made single-unit recordings in a human and found an "anterior color center" whose responses corresponded to color perception.

Functional role and the definition of early visual areas

In defining visual areas, it is reasonable to assume that each visual area with retinotopic organization should have a complete map of the visual field (Zeki, 2003) and homogenous functional response properties across the visual field representation. The color and form selectivity of V4 neurons, shown in both macaque and in human, suggests that V4 is specialized for mid-level form vision, including but not limited to the processing of color (for example, see Arcizet, Jouffrais, & Girard, 2009; David, Hayden, & Gallant, 2006; Dumoulin & Hess, 2007; Gallant, Braun, & van Essen, 1993; Gallant, Connor, Rakshit, Lewis, & van Essen, 1996; Kumano, Tanabe, & Fujita, 2008; Mysore, Vogels, Raiguel, & Orban, 2008; Pasupathy, 2006; Thielscher, Kölle, Neumann, Spitzer, & Grön, 2008; Vinberg & Grill-Spector, 2008; Wilkinson et al., 2000). V4 is also reported to be more greatly influenced by attention than earlier areas, in both macaque and human (Haenny & Schiller, 1988; Hansen et al., 2007; Kastner, Weerd, Desimone, & Ungerleider, 1998; Maunsell, 1995; Maunsell & Cook, 2002; McAdams & Maunsell, 1999; Mehta, Ulbert, & Schroeder, 2000; Moran & Desimone, 1985; Schwartz et al., 2005; Tootell et al., 1998). Some functional properties of human ventral V4 and its putative dorsal component have previously been measured in an attempt to differentiate between the alternative models of human V4, as outlined below.

Using a model similar to that presented by Hansen et al. (2007), Tootell and Hadjikhani (2001) report a human V4v that represents a quadrant of the contralateral hemifield and define V4d as the corresponding dorsal area that represents the lower quadrant. However, they also argue that while these areas are complementary in their visual field coverage, they do not share common functional selectivity. Specifically, they report that while V4d responds to kinetically defined contours, V4v does not. They also tested color selectivity but found that neither V4v nor V4d preferred chromatic to luminance-defined stimuli; instead, they found strong chromatic selectivity only in the part of the ventral occipital cortex that they term V8.

Hansen et al. (2007) measured the degree of attentional modulation across human visual cortex to compare the functional properties of human V4v and putative V4d with surrounding areas. Subjects were scanned while covertly attending to a series of wedges, and spatial tuning in some areas tended to shift toward the location of the attended stimulus. Hansen et al. found that these attention-induced shifts in spatial tuning were greater in LO than in V4v and V4d and greater in V4v and V4d than in V3. They argue that the intermediate magnitude of attentional modulation in V4v and V4d is consistent with these regions constituting a single visual area.

Wade, Augath, Logothetis, and Wandell (2008) compared the response of human and macaque V4 to colored Mondrian stimuli, using fMRI. In macaque, they found similar responses to color in ventral and dorsal V4. In humans, they found a strong response to color in ventral V4, consistent with earlier reports, and also found some evidence of a response to color in the area corresponding to V4d as defined by Hansen et al. (2007). The dorsal color response was weak, but there were "some hints of response" in the location corresponding to putative V4d. Wade et al. (2008) also note that it is conceivable that any preference for color in V4d may have been overlooked by previous studies because of its smaller size, compared with V4v.

Scope of the current study

Since V4 has been implicated in processing color, here we tested the color response of human occipital cortex using fMRI. We tested for voxels that showed a larger response to colored stimuli than to grayscale stimuli of the same luminance. We used complex stimuli (movie clips), which, unlike many previous investigations of color selectivity (Beauchamp et al., 1999; Lueck et al., 1989;

McKeefry & Zeki, 1997; Wade et al., 2008), have a wide range of spatial and temporal frequencies and contain naturalistic visual objects, including people, while typically containing a greater variation of image content than standard natural image databases (Bex, Solomon, & Dakin, 2009). In using these stimuli, we hoped to maximize the chance of eliciting any color-sensitive response from ventral V4, in order that we might compare this functional response with its suggested dorsal counterpart. We combined these measures of color responsiveness with functionally defined retinotopic maps, acquired separately in high-resolution scans. Although previous studies have used naturalistic stimuli to measure color response (Bartels & Zeki, 2000, 2004), these earlier studies did not use retinotopic mapping. By defining the early visual areas retinotopically, we can compare the color responsiveness of V4 according to the V4v/V4d and ventral hemifield models.

In summary, Hansen et al. (2007) argue for the dorsal component model of human V4 on the basis of visual field coverage, homology with macaques, and similarity in attentional modulation. Here, we consider both the visual field coverage of V4 according to the two models, as well as the functional response properties of the suggested dorsal and ventral parts of V4 to colored versus achromatic stimuli.

Materials and methods

Subjects

Data were collected on six subjects (three male), aged between 25 and 40 years, with normal or corrected-to-normal visual acuity and normal color vision, as tested using Ishihara plates (Ishihara, 1990). Four of the subjects (all except DM and KS, who were unavailable at the time of the test) were also found to have normal color vision when tested with the Hardy–Rand–Rittler pseudoisochromatic plates (HRR, 4th edition, published by Richmond Products). All subjects provided informed consent, and the entire study was carried out in accordance with the guidelines of the University of Sydney Human Research Ethics Committee.

Chromatic, spatial, and temporal stimulus properties

We used retinotopic mapping to define early visual areas and then tested the responsiveness of these areas to chromatic over achromatic stimuli. We used standard stimuli to derive maps of polar and eccentricity preferences and then chromatic and achromatic versions of the movie *Strictly Ballroom* to test the responsiveness of these areas to chromatic and achromatic stimuli.

Rotating wedge and expanding ring stimuli

For retinotopic mapping, we used standard rotating wedge and expanding ring stimuli to find the preferred polar angle and eccentricity preference of each voxel (Engel et al., 1994; Schira, Tyler, Breakspear, & Spehar, 2009; Wandell et al., 2007). Sample frames of the rotating wedge and expanding ring stimuli are shown in Figures 2A and 2B, respectively. The rotating wedge stimulus consisted of a black and white checkerboard in a 45° wedge centered on

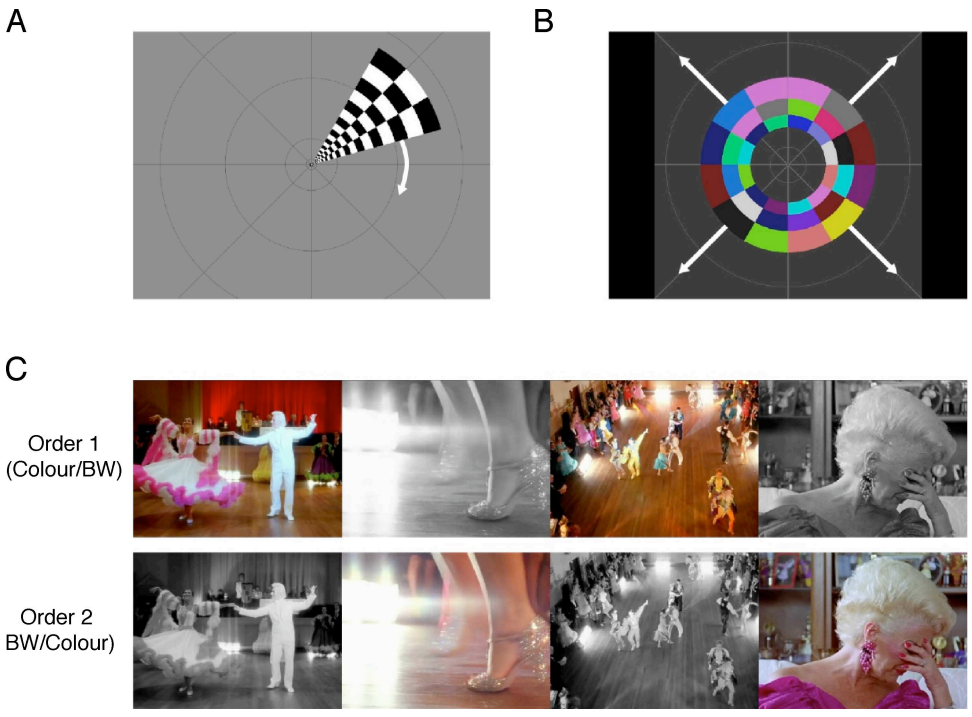

Figure 2. (A, B) Stimuli used to map visual field coverage and (C) color responsiveness.

a fixation marker at the center of the screen and with an overall radius of half the height of the screen. The checks evenly divided the wedge into three smaller wedges, and each of these 15° wedges was further divided into 20 ring segments. The wedge rotated in increments of 15°, once every 1.5 s. As it rotated, the checks of each 15° segment of the wedge moved smoothly toward or away from the central fixation marker, with the direction of movement alternating with each segment. The width of each ring segment increased logarithmically with distance from the center, as illustrated in Figure 2A. Subjects each completed four runs of 6.45-min duration: two where the wedge rotated clockwise and two where the wedge rotated counterclockwise.

The ring stimulus was made up of the same checkerboard pattern as the wedge stimulus, except that instead of black and white checks the checks were randomly chosen colors, and the checks did not move but updated with a new color at a rate of 8 Hz. The ring always had an annulus of 3 ring segments and expanded by one ring segment every 1.8 s, cycling through the entire range of ring sizes every 36 s. Each subject completed at least two runs of 6.45-min duration.

Both the wedge and ring stimuli were drawn on a background with a fixation cross of thin gray lines, as shown in Figure 2. Subjects were instructed to fixate at the central point of the stimulus and, in the case of the rotating wedge stimulus, were required to perform a dimming task at fixation. Differences between the wedge and ring stimuli (such as the use of color in the ring stimuli) were not theoretically motivated but were due to the fact that the eccentricity maps were acquired using an earlier protocol.

Chromatic vs. achromatic stimulus

To compare the response of early visual areas to chromatic vs. achromatic stimuli, we generated chromatic and achromatic versions of a commercial DVD movie. We used Baz Luhrmann's *Strictly Ballroom* (1992, M&A Film, Australian Film Finance) and selected a section of the movie that contained a range of depths, objects, people, and colors. We chose to use a movie instead of a simpler stimulus in order to improve the likelihood of evoking a color-sensitive response across neurons that prefer a range of (for example) spatial and temporal frequencies and orientations. Sample frames from the selected clip are shown in Figure 2C.

The second chapter of *Strictly Ballroom* was extracted as an uncompressed avi file using Handbrake software (http://handbrake.fr/). Frames were extracted from the avi file using Matlab (version 7), and the RGB values of each frame were stored separately. Next, to create an achromatic version of each frame, we determined the photopic luminance of each RGB value in the frame and substituted this RGB with a gray value (R = G = B) of the same photopic luminance (determined using the Stockman & Sharpe, 2000, 2-degree luminosity function and calibrated for our display apparatus). Once achromatic versions of each frame were generated, the frames were recombined into avi files of 2 min each. Two versions of the movie clip were created: both had the same 2-min continuous segment of the movie and alternated between chromatic and achromatic stimuli every 15 s. For the first version, the movie started in color (Color/BW order), and for the second version, the movie started in black and white (BW/Color order). Half of the movie (odd numbered blocks) were seen first in color, while the other half (even numbered blocks) were seen first in black and white.

Experimental scans using the chromatic vs. achromatic stimuli were completed during a single session for each subject. The session included four functional scans, each lasting 4.5 min. During each scan, the subject viewed 18 blocks of the experimental stimulus, consisting of 2.25 loops of either the Color/BW (on odd numbered scans) or the BW/Color clip (on even numbered scans). Throughout all experimental scans, subjects were instructed to maintain fixation on a central point and performed a dimming task at this location.

Fixation task

Throughout the wedge and the chromatic vs. achromatic scans, subjects performed a dimming task at fixation in order to ensure they maintained fixation. In the center of the screen, a small cross (height: 0.2 degree visual angle) was drawn on a circular gray background. Throughout each scan, the cross switched between white and black at an average rate of 1 Hz, with random jitter of up to 300 ms added to the switch times. Subjects responded by pressing a button at the onset of a black cross and releasing it when the cross switched to white.

Color calibration procedures and display system

Stimuli were generated and displayed using Matlab (version 7) software in conjunction with routines from PsychToolbox 3.0.8 (Brainard, 1997; Pelli, 1997) on a Dell Latitude laptop computer driving an nVidia Quadro NVS 110M graphics card to draw stimuli to a Dell 5100 MP projector, which projected the images through a Faraday shielded window onto a translucent Perspex screen. Subjects, while lying in the scanner, viewed the Perspex screen through a mirror mounted above the head cage that reflected the image from the screen located behind the scanner. The screen was viewed from a distance of 167 cm, and the image subtended an area of 18.7 by 13.3 degrees visual angle. Stimuli were calibrated

in situ for the DLP projector and screen arrangement, using measurements of the screen obtained from the doorway of the scanning room with a PR-655 SpectraScan spectrophotometer (by Photo Research). Scanning took place in a darkened room.

Changes in both chromaticity and luminance of the screen with increasing R, G, and B values, along with interactions between the G + B (C), R + B (M), R + G (Y), and R + G + B (K) channels, were taken into account when generating the experimental stimuli. Modeling the interaction between channels was of particular importance for our DLP projection system that rendered each RGB input using four channels (R, G, and B channels, along with a white channel to boost luminance). The CIE (*xyY*) coordinates were calculated using the Stockman and Sharpe (2000) 2-degree cone spectral sensitivities for each of the seven sets of 16 points measured during calibration, and each of these was interpolated to 255 values using the best fitting spline. The spline fits were then used to calculate the luminance and chromaticity for each combination of R, G, and B intensity values using the masking model described in Tamura, Tsumura, and Miyake (2003). These measurements of luminance were used in the process of creating an achromatic version of each movie frame, as described above.

fMRI methods

fMRI data were collected using a 3T Philips scanner (St. Vincent's Public Hospital, Sydney, Australia), with a birdcage head coil.

Anatomical measurements and definition of gray matter

The anatomical image for each subject was generated from the average of three scans. Two of these were high-resolution (1 × 1 × 1 mm) structural MR images of each subject's whole brain, acquired using a Turbo Field Echo (TFE) protocol for enhanced gray–white contrast. A third, higher resolution (0.75 × 0.75 × 0.75 mm) scan of the caudal half of the head was also acquired in order to recover more anatomical detail of the occipital lobes.

Using the Statistical Parametric Mapping (SPM) software package SPM5 (described in detail by Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997), anatomical images were each reoriented to approximately the same space using anterior and posterior commissures as anatomical landmarks. Fine alignment of these anatomical images was carried out using normalized mutual information based coregistration, and all of the anatomical images were resampled so that they were in the same voxel space with a resolution of 0.75 × 0.75 × 0.75 mm. From each image, we removed intensity inhomogeneities using a non-parametric inhomogeneity correction method (Manjón et al., 2007) and normalized the images such that the white matter had approximately equal intensity. The coregistered, inhomogeneity corrected, normalized images were then averaged together to produce a mean anatomical image for each subject.

ITKGray software (Yushkevich et al., 2006) was used to specify the white matter of each subject, initially using automatic segmentation tools, then using manual editing. The segmentation image was imported into mrGray, part of the mrVista software package developed by the Stanford Vision and Imaging Laboratory (http://white.stanford.edu/software/). In mrGray, gray matter was "grown" out from the white matter in a sheet with a maximum thickness of 4 voxels.

Functional measurements

fMRI data were acquired using a T2*-sensitive, FEEPI pulse sequence, with echo time (TE) of 32 ms, time to repetition (TR) of 3000 ms, flip angle of 90°, and field of view of 192 mm × 69 mm × 192 mm. The standard retinotopy measurements (wedge and ring stimuli) were acquired in 46 slices of 1.5-mm thickness, with effective in-plane resolution of 1.5 mm × 1.5 mm. The color vs. black and white stimuli were acquired in 33 slices of 2-mm thickness, with effective in-plane resolution of 2 mm × 2 mm. Slices were collected in an interleaved, ascending order, in a coronal plane tilted such that the scan covered the whole of the occipital lobe and the posterior part of the parietal and temporal lobes. Using SPM5, all functional data were preprocessed to correct for slice time and head motion before alignment to the structural data. Data from functional scans were aligned to a whole head anatomical scan acquired in the same session, using normalized mutual information-based coregistration. The functional data from chromatic vs. achromatic scans were then aligned to the data from the wedge and ring scans (which were acquired in a separate session) by first aligning the within session anatomical from one to the within session anatomical of the other, then applying the same transformation to the functional data. Data from the first and last 15-s blocks in the chromatic vs. achromatic scans were excluded from this analysis, and data were labeled with the stimulus (color or black and white) occurring 6 s previously in order to approximately compensate for hemodynamic lag.

Definition of retinotopic areas

Visual areas were defined retinotopically using data from the wedge and ring stimuli (described above). Data from clockwise-rotating wedge runs were temporally reversed before averaging with data from the counterclockwise-rotating wedge runs. Average data from both wedge and ring runs were smoothed with a Gaussian kernel of 1.5-mm half-width, then projected onto a computationally flattened representation of the cortex for each hemisphere of each subject, using mrVista. The resultant polar angle and eccentricity preference maps for each subject are shown in Figure 3.

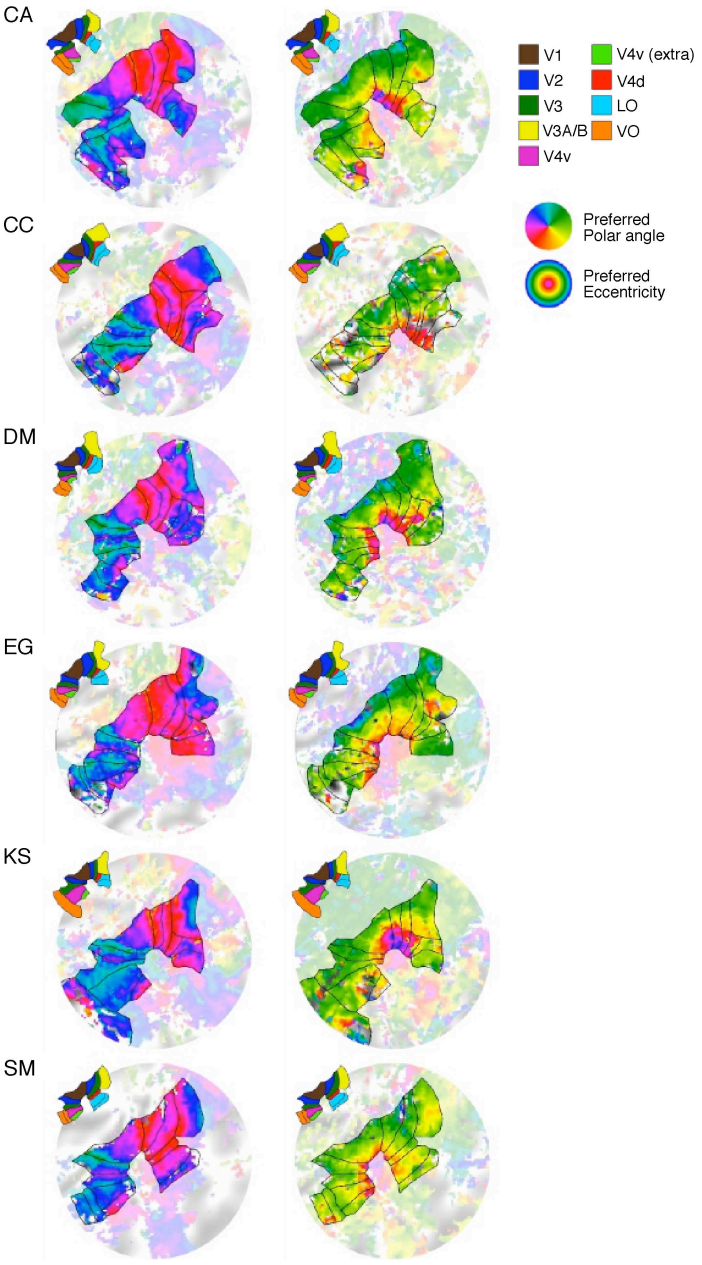

Figure 3. (Left) Polar angle and (right) eccentricity maps for the right hemisphere of each of the six subjects. Key to the top left of the polar angle maps indicates the location of the early visual areas (for details of definition, see text). Cortical regions outside the retinotopically defined areas are shown in lower contrast.

Retinotopic maps for each subject are shown in Figure 3. Areas V1, V2, V3, and V3A/B were manually defined on the phase and eccentricity maps derived from the wedge and ring stimuli, using the conventions common to Brewer et al. (2005), Hansen et al. (2007), and Larsson and Heeger (2006). According to these definitions, the foveal representation at the occipital pole is shared by V1, V2, and V3, while V3A and V3B, which border the dorsal part of V3, share a dorsal fovea. For our analysis, we did not attempt to separate V3A and V3B.

We defined areas hV4, LO1, and LO2 according to the conventions of Larsson and Heeger (2006), where hV4 is a hemifield representation of the contralateral visual field sharing a border with the ventral part of V3 and sharing the foveal representation of V1, V2, and V3. In Figure 3, hV4 is given by the union of V4v and V4v (extra). Areas LO1 and LO2 both have a hemifield representation and extend laterally from V3d. In Figure 3, LO1 and LO2 comprise the regions in red and light blue, and the boundary between them is drawn as a black line in the light blue section. LO1 includes both the red region and the light blue section bordering V4d; LO2 is the more lateral of the light blue sections.

We used the definitions of Hansen et al. (2007) to define ventral and dorsal V4 (V4v and V4d) and area LO. According to these conventions, V4v extends laterally from the ventral border of V3v, where the upper vertical meridian is represented, and shares the foveal representation of V1, V2, and V3. V4v includes a representation of the contralateral upper visual field, and the contralateral horizontal meridian, extending slightly into the lower visual field. V4d represents the remaining part of the contralateral visual field, with a lower vertical meridian representation along its border with V3d. Hansen et al. (2007) describe the visual field coverage of V4v as intermediate to a quarterfield and a hemifield but allow for individual variation in the precise coverage. Based on the sample subjects given in Figure 4 of Hansen et al. (2007), we defined V4v as covering halfway between a quarterfield and a hemifield, including the upper 3/4 of the contralateral visual hemifield, and V4d as covering the lower quarter of this hemifield. For subject EG, where the V4d/LO boundary was not clearly defined on this criterion, we chose a boundary that resulted in the relative sizes of V4d and LO approximately matching the ratio in other subjects and in the sample subjects of Hansen et al. (2007). V4d also borders V3A/B. According to Hansen et al. (2007), LO shares a border with V4d and extends laterally but is not clearly defined on the basis of its retinotopic organization. Herewe defined LO as the union of LO1 and LO2 (as defined above) minus the area defined as V4d, that is, the entire light blue section in the maps in Figure 3.

For areas VO1 and VO2 (not shown in Figure 1 but drawn on maps in Figure 3), we followed the conventions of Brewer et al. (2005), defining VO1 as a hemifield representation (where it existed), extending ventrally from V4v, and VO2 as a hemifield representation extending ventrally from VO1. VO1 and VO2 share a foveal representation that is separate from the main foveal confluence at the occipital pole.

Assessing the chromatic vs. achromatic responsiveness of each voxel

We used the response of each voxel during scans where subjects were viewing clips from the film *Strictly Ballroom* to assess color responsiveness. Averaged data from

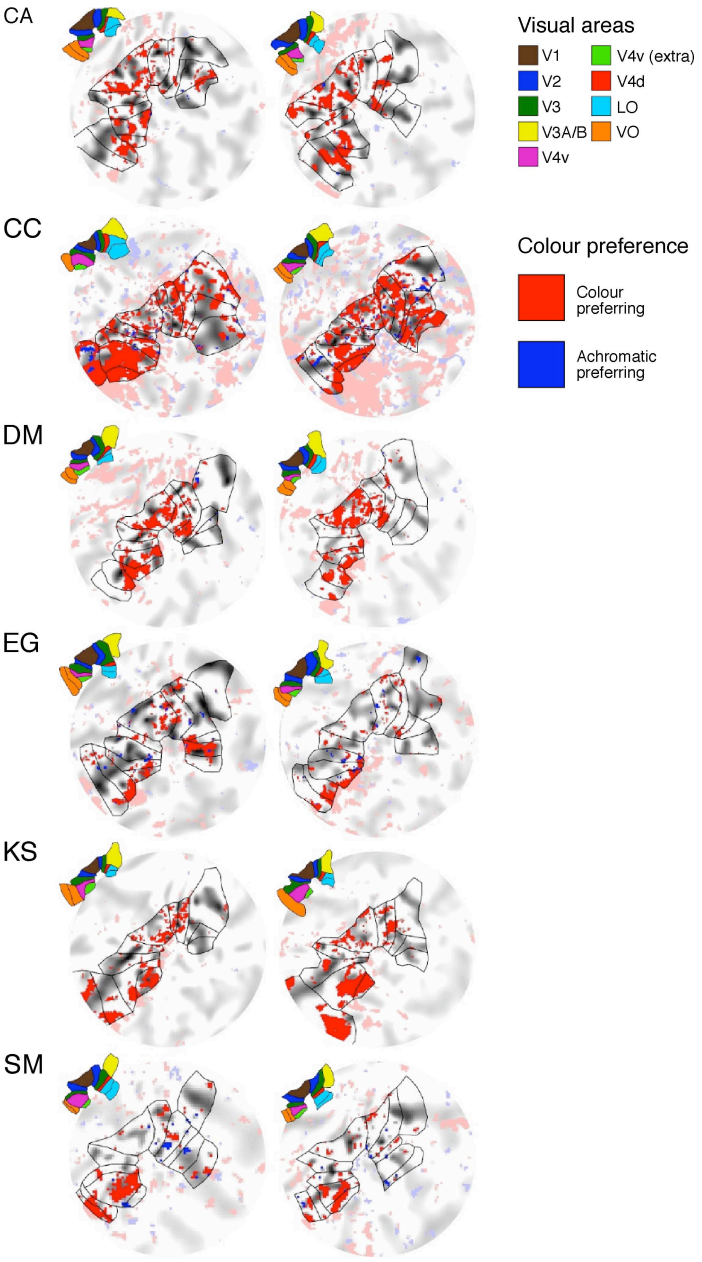

Figure 4. Maps of color response across all visual areas for each subject. Data from both the left and right hemispheres of each subject are shown on the flattened cortical maps to the left and right, respectively. Only those voxels where there was a coherent response alternation at the rate of the stimulus alternation (period of 30 s) are shown in color. The threshold coherence level was set for each subject as one standard deviation above the mean coherence across visual areas. Voxels that responded preferentially to color blocks are in red, and those that preferred achromatic blocks are in blue. As in Figure 3, the key in the top left of each hemisphere indicates the identity of each visual area, and regions outside the retinotopically defined areas are shown in lower contrast.

the color and black and white blocks were smoothed with a Gaussian kernel of 1.5-mm half-width, and the mrVista *corAnal* tool was used to find, for each voxel, the coherence and phase of the harmonic of its response corresponding to an alternation with stimulus color (with a period of 30 s). To generate the maps showing chromatic responsiveness in Figure 4, voxels were thresholded according to the coherence of the harmonic for each subject in relation to the average coherence across all visual areas; only voxels for which the coherence exceeded one standard deviation above the mean were included. Those voxels that met this criterion were then partitioned into "chromatic preferring" and "achromatic preferring" according to the phase of the harmonic, which corresponded to whether their response was greater in the color or achromatic blocks of the stimulus.

In order to compare areas quantitatively, we compared the amplitude of each area's response modulation with the color/achromatic cycle of the stimulus. The average response (% signal change across all voxels) of each area was Fourier transformed, and the Fourier component at the same frequency as the color/achromatic cycle (30 s) was projected onto a reference vector of unit amplitude, whose phase corresponded to a positive modulation during the color blocks. Using this method, a tendency for the BOLD response to be greater during color blocks results in a positive value, while a tendency for the BOLD response to be greater during achromatic blocks results in negative values. The amplitude of the projected vector was then divided by the average amplitude across all Fourier components (all frequencies) to give a normalized value.

Results

We defined the early visual areas of each subject on the basis of polar angle and eccentricity preference, then found the responsiveness across the early visual areas to chromatic vs. achromatic stimuli. The maps of polar angle and eccentricity preference that were used to retinotopically define visual areas for each subject are shown in Figure 3. The criteria used to define each area retinotopically are described in the Definition of retinotopic areas section above.

Generally increased responsiveness to color over achromatic stimulus blocks

Figure 4 shows all voxels for which there was a response modulation with stimulus color changes, that is, which showed a coherent response modulation with a period of 30 s, corresponding to two blocks from the stimulus (see Methods section for more details).

For most subjects, there were very few voxels that showed an increased responsiveness to grayscale over

color stimuli (shown in blue in Figure 4). Since the color stimuli included the same luminance contrast as the achromatic stimuli, the lack of voxels showing an increased responsiveness to achromatic over color stimuli is unsurprising; voxels that responded only to luminance variation should show the same response to both types of stimulus rather than an increased response to the achromatic blocks.

Color response of area V4 and its putative dorsal component

The response of the ventral part of V4 (V4v) showed a modulation with the color/achromatic cycle of the stimulus: the BOLD response in V4v was greater during chromatic than achromatic blocks. The average modulation across V4v can be seen in the leftmost plots of Figures 5A and 5B for each subject and averaged across subjects, respectively. Voxels lateral to V4v (V4v extra), included in the ventral hemifield model of V4 but not the split dorsal/ventral model, showed a similar modulation to that seen in V4v, as seen in the middle plots of Figure 5. In contrast, V4d did not show a modulation with the color/achromatic cycle of the stimulus, as seen in the relatively flat response across time in the rightmost plots of Figure 5. We analyzed the variance in the response within these areas (plotted in Appendix A) to test whether V4v and V4d differed in their overall responsiveness: we used an analysis of the variance of the response to capture the peaks and troughs of the data without requiring a measure of baseline activity. We found that the difference between V4v and V4d cannot be attributed to their overall responsiveness but demonstrates a difference in the responsiveness to chromatic stimuli.

The difference in color responsiveness between V4d and V4v is also seen in Figure 6A, where we plotted the Fourier amplitude of each area's response at the frequency corresponding to the color/achromatic stimulus modulation, projected onto a reference vector of relevant phase to show the extent to which each area responds more strongly to color than to achromatic blocks. Using a paired two-tailed *t*-test to compare the normalized Fourier amplitude values for areas V4d and V4v, we found that the color responsiveness of V4v was significantly greater than V4d ($p < 0.01$, $t(5) = 5.86$).

We also analyzed the color responsiveness of each area using an alternative measure: the percentage of voxels that showed a reliable modulation with stimulus color. The results of this alternative analysis, shown in Appendix A, were similar to those plotted in Figure 6.

Finally, we also repeated our main analysis using only data from the second half of the experimental run, to test the possibility that our data included an artifact from a primacy effect (where the response of the first viewing of

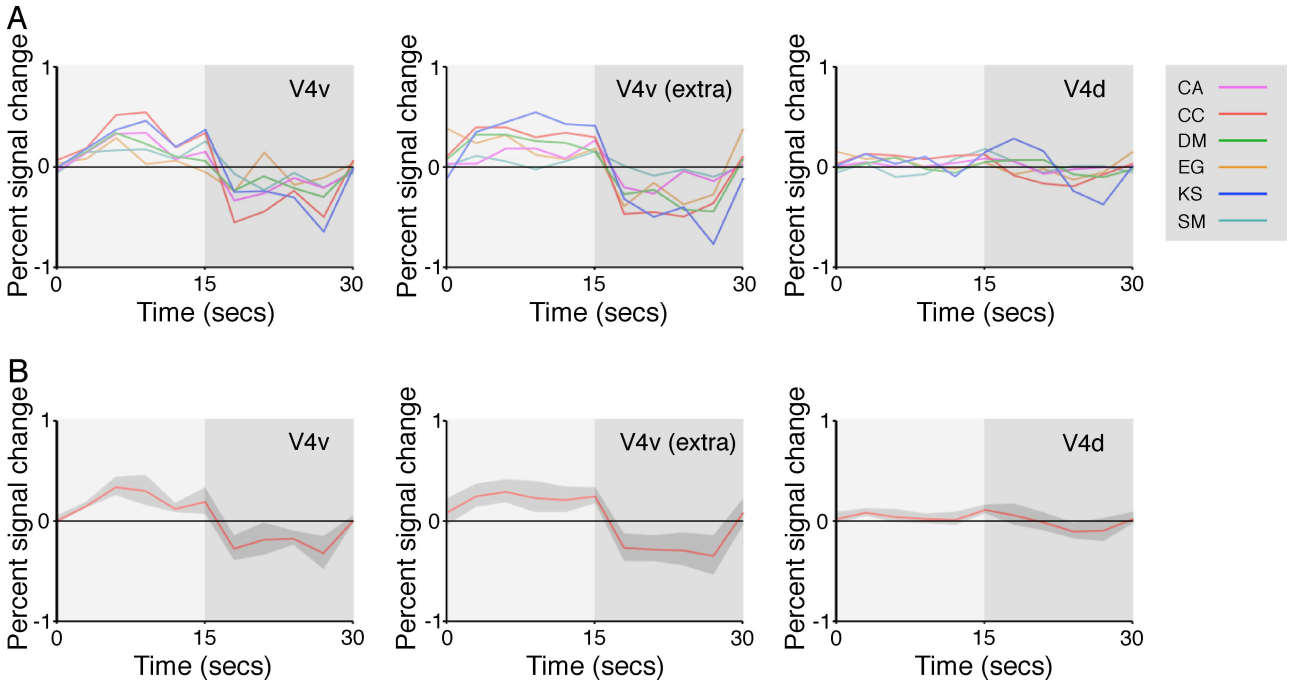

Figure 5. Average response across all voxels in areas V4v, V4v (extra), and V4d to color and achromatic stimuli, (A) for individual subjects and (B) averaged across 6 observers. BOLD response (% signal change) was averaged across each 30-s cycle from all runs. Each cycle is aligned such that the first 15 s (shaded in light gray) are the response to the chromatic stimuli and the second 15 s (shaded in darker gray) are the response to the achromatic stimuli. The mean response across observers is shown as a red line in (B), and the gray areas indicate the mean ± 2 between-subjects standard error (95% confidence intervals) for the average across observers.

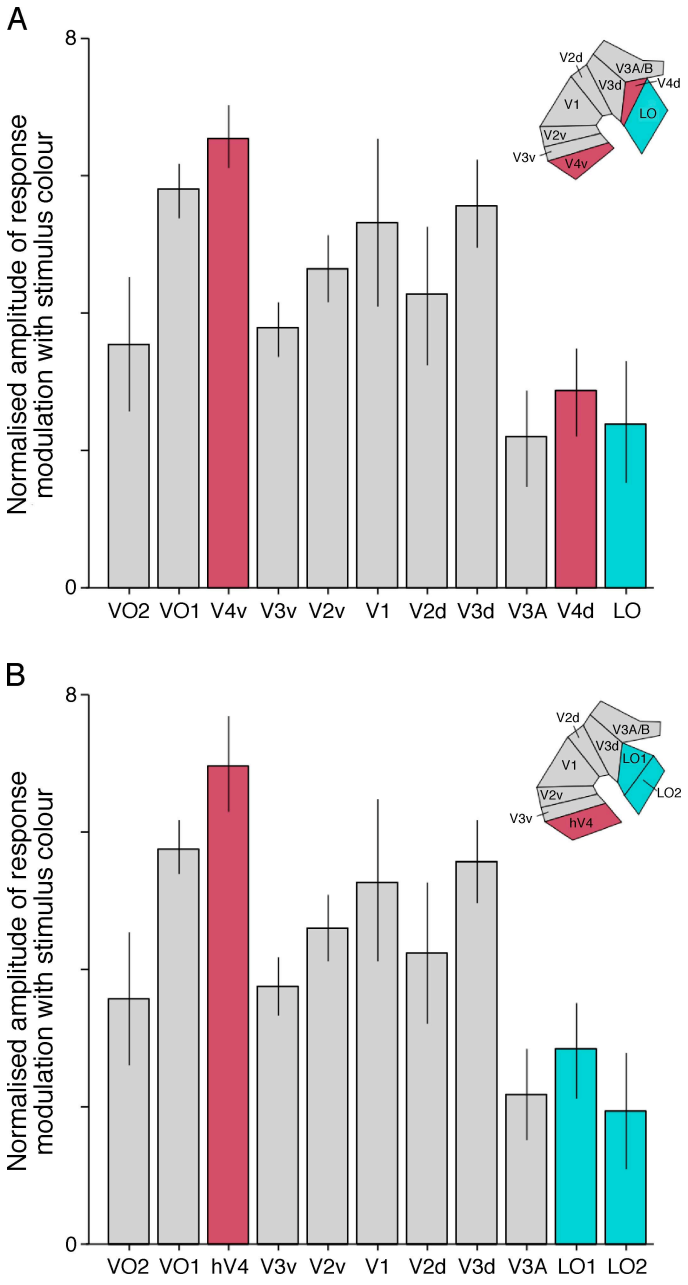

Figure 6. Color responsiveness of each area, according to (A) the split dorsal/ventral model of V4 and (B) the ventral hemifield model of V4. There was a general trend for color responsiveness to be highest in ventral areas, lowest in dorsal areas, and intermediate in areas V1, V2, and V3. The bars indicate the extent to which each area shows a reliable response modulation with stimulus color. The average response (% signal change) of each area was Fourier transformed, and the Fourier component at the same frequency as the color/achromatic cycle (30 s) was projected onto a reference "color preferring" vector. Positive values indicate a stronger response to color, and negative values indicate a stronger response to achromatic blocks. This projected component was then divided by the average amplitude across all frequencies to give the normalized amplitude reported above. Error bars show 95% confidence intervals (the mean ± 2 standard error) of the between-subjects mean.

each stimulus block was enhanced relative to subsequent viewings). In this final analysis, shown in Appendix A, we again found a similar pattern of results.

In summary, the difference between V4v and V4d in their response to these color and achromatic stimuli, shown here using a variety of measures, is inconsistent with their belonging to a single visual area.

If human V4 is split into ventral and dorsal components (Figure 6A), then the single area comprises a ventral part of high color responsiveness and a dorsal part of lower color responsiveness, and area LO is a single area of low color responsiveness.

If instead human V4 is a single ventral hemifield representation (Figure 6B), then hV4 is an area of high color responsiveness and LO comprises two subparts (LO1 and LO2) that both show lower color responsiveness than areas V1, V2, and V3. Considering only the assumption that visual areas should have common functionality, these data argue in favor of the single hemifield model of V4.

Visual field coverage according to the hemifield and split dorsal/ventral models of V4

To compare the two models of human V4 on their visual field coverage, for each area we derived plots of their coverage according to the definitions of the two models, shown in Figure 7. These maps include a dot for each voxel in the region of interest, with placement determined by the preferred phase of the response to the wedge (polar angle) and ring (eccentricity) stimuli. For this analysis, we used the same area definitions shown in Figure 3, but we used the averaged data prior to spatial smoothing.

Visual field coverage was generally good in areas V1, V2, and V3, although there was inter-subject variation in the patchiness of coverage. Area V4v, common to both models of V4, provided good coverage of the visual field above the horizontal meridian, extending slightly below the meridian in both left and right quadrants. This coverage is consistent with the parameters used to define area V4v (see Methods section).

The critical area of difference between the models is how well they account for coverage in the remaining part of the visual field, assuming that area V4 should contain a complete representation. In the split model, the dorsal part of V4 should represent the lower vertical meridian and its surrounds. In the single hemifield model, this part of the visual field should be covered by extending the ventral border of V4v, tested in this study by the inclusion of the additional area labeled V4v (extra) in Figure 7.

For clarity, visual field coverage within the common area (V4v) and the areas of difference (V4d and V4v (extra)) are plotted separately above the maps of coverage by areas V4 and hV4. Both V4d and V4v (extra) have

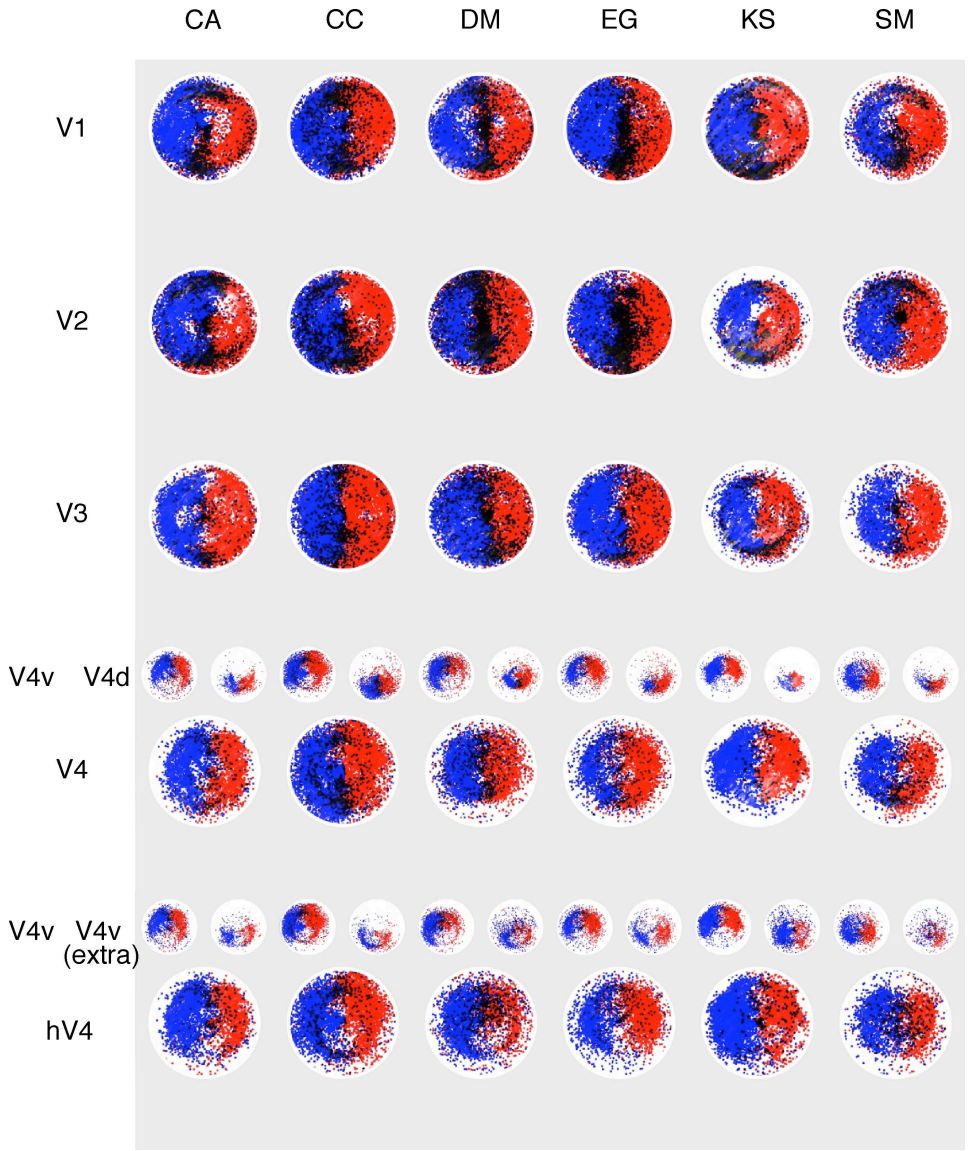

Figure 7. Visual field coverage of V1, V2, V3, and V4 according to the split dorsal/ventral model of V4 (V4v + V4d = V4) and the ventral hemifield model of V4 (V4v + V4v (extra) = hV4). Each dot corresponds to the visual field preference of one voxel, either from the left hemisphere (red dots) or right hemisphere (blue dots). The intensity of each dot was scaled according to the coherence of its visual field preference, from white (incoherent) to red/blue (0.7 coherence value or higher, where 1 is the maximum). Areas where the red and blue dots overlap sum to black.

voxels that respond to the lower part of the visual field that is not covered by V4v. Unlike Hansen et al. (2007), we found that visual field coverage according to the ventral hemifield model of V4 is not clearly deficient, weakening the claim that V4 must include V4d for this area to have coverage of the entire visual field.

Retinotopic organization within dorsal visual cortex does not clearly support either model of human V4

A final point of difference in the predictions of the two models of human V4 is in the organization of dorsal visual cortex lateral to V3d. We tested whether the retinotopic data we collected could be used to offer support to either model of human V4. Specifically, the split V4v/V4d model presented by Hansen et al. (2007) predicts that area LO has unstructured retinotopy and that V4d shows a smooth progression from the lower vertical meridian at its boundary with V3d to an angle intermediate to the horizontal and lower vertical meridians. The LO1/LO2 model of this area, as outlined by Larsson and Heeger (2006), predicts that both LO1 and LO2 have complete hemifield representations. Area LO1 progresses from the lower vertical meridian at the V3d border to the upper vertical meridian at the LO1/LO2 border, where a reversal occurs. Area LO2 progresses from the upper vertical

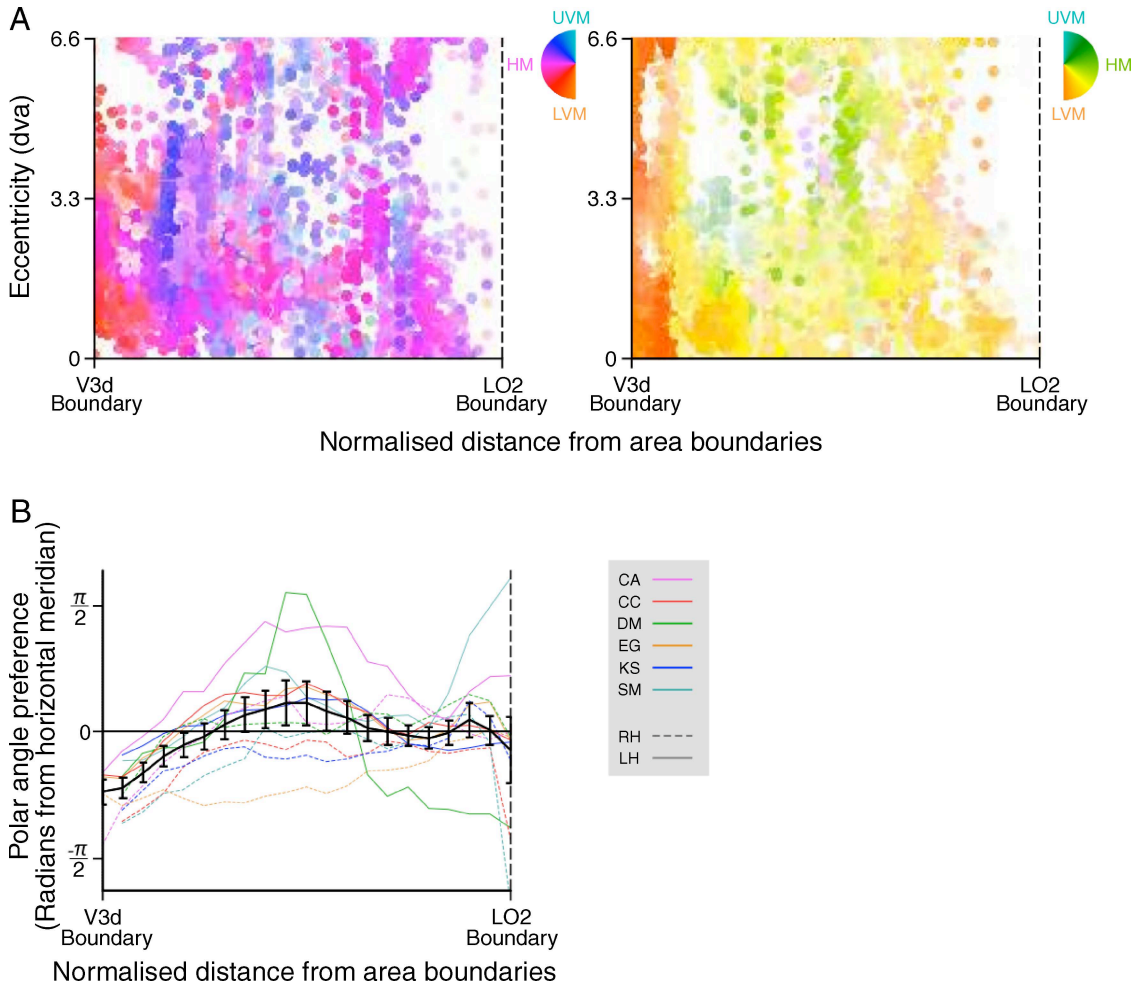

Figure 8. (A) The preferred angle and eccentricity of each voxel within V4d and LO (or LO1 and LO2) is shown for a sample subject (CC), following similar conventions to Larsson and Heeger (2006, their Figure 8B). Data from right and left hemispheres are shown on the left and right plots, respectively. Each dot is positioned according to its preferred eccentricity and its relative distance in the flattened cortical maps from the V3d/V4d boundary and the furthermost edge of LO2. The color of each dot is determined by its preferred polar angle (see key to upper right of each plot), and the color's saturation corresponds to the coherence of each voxel's preference for that polar angle, with more saturated colors indicating a clearer preference for that polar angle. (B) The data for each subject (12 hemispheres) were collapsed across preferred eccentricity and the mean polar angle preference is plotted following similar conventions to Larsson and Heeger (2006, their Figure 8C). In (B), the polar angle preference of 0 corresponds to the horizontal meridian, and $\pi/2$ and $-\pi/2$ correspond to the upper and lower vertical meridians, respectively. Data for each hemisphere are plotted as a thin line, and the mean across 12 hemispheres is plotted as the thicker black line (±1 standard error of the mean).

meridian at its border with LO1 to a lower vertical meridian representation.

In Figure 8, we show polar angle preference in the relevant part of dorsal visual cortex from our data. Our data do not clearly support the V4d/LO model, where area V4d has an orderly map of the lower part of the contralateral hemifield, but LO is unstructured in its retinotopy. Near the V3d boundary (within V4d), we found selectivity for the lower part of the contralateral hemifield, but we did not find that this structure broke down upon reaching a point between the lower vertical meridian and the horizontal meridian. Instead, there was a smooth progression to an average polar angle preference above the horizontal meridian, before a reversal. This evidence of weak structure within the area corresponding to LO according to the V4d/LO model argues against the split V4v/V4d model of human V4.

However, while our results do not clearly support the V4d/LO model of this part of the cortex, neither do they clearly support the LO1/LO2 model. The average data show a tendency for the polar angle preference to progress smoothly from the V3d boundary to above the horizontal meridian (corresponding to the LO1/LO2 boundary), but they do not approach the upper vertical meridian as

predicted by the LO1/LO2 model. Within area LO2, the LO1/LO2 model predicts a hemifield representation progressing from the upper vertical meridian at the LO1/LO2 border to the lower vertical meridian. While our data showed a trend in this direction, the data within this area were inconsistent across hemispheres. Larsson and Heeger (2006), who analyzed data from fifteen rather than six subjects, found a clearer pattern in support of their model but also did not find an average preference for either vertical meridian at the edges of LO1 and LO2. They offer an explanation for this in terms of the effects of spatial averaging of neuronal signals inherent in the BOLD response, which will cause the measured average to be shifted toward the horizontal meridian.

In summary, we found that our retinotopic mapping data did not clearly support or exclude the predictions of either model in regard to the organization of dorsal visual cortex. Although the split V4v/V4d and ventral hemifield models of human V4 make contradicting predictions, we were unable to use these predictions to find clear evidence in favor of either model over the other in our data.

Discussion

We used fMRI to investigate the organization of color responsiveness across early visual cortex, with the particular aim of testing whether the response of ventral V4 matches that of its putative dorsal component. We compared the BOLD response of human occipital cortex to colored movie segments vs. grayscale versions of the same segments. Across all early visual areas, there were voxels that preferred color stimuli and very few voxels that preferred achromatic stimuli, consistent with stimuli that were closely matched in luminance content. There were generally more voxels that preferred color stimuli in ventral than dorsal areas. Of particular relevance to this study, we found a strong color-sensitive response in ventral V4 but not in its putative dorsal component. Thus, although the results in this study regarding the retinotopic organization of dorsal visual cortex do not distinguish single or split area V4 in humans, the difference in functional responsiveness of the two regions to color modulation supports the idea that human V4 consists a single area in the ventral occipital cortex.

Ventral V4 shows an increased response to colored stimuli, dorsal V4 does not

We found that the dorsal region proposed to be part of V4 by Hansen et al. (2007) showed one of the lowest color responses, while ventral V4 showed the highest of the areas considered (as illustrated in Figure 6). This functional difference argues against these two parts of the cortex comprising the same visual area.

The color responsivity of V4v that we found here is contrary to the findings of Mullen et al. (2007) and Tootell and Hadjikhani (2001), who reported color response in areas around V4v but no color response in V4v itself. We believe that the difference is one of sensitivity and that the stimuli we used were particularly suited to revealing the strong color response in these ventral areas since they have the advantage of being complex, naturalistic stimuli, which should put the human visual system into its natural operating range. However, we did find slightly higher color responsiveness in the area ventral to V4v, as seen in Figure 6, in that the addition of the extra part of V4v slightly increased the color responsiveness of hV4 relative to V4v alone.

The low color responsiveness of V4d and LO (or LO1 and LO2) is consistent with these areas being functionally similar, although the response of the dorsal areas when taken alone does not provide strong evidence for one model over the other.

There was a general bias for ventral areas to show a greater color response than dorsal areas, but the difference between V4v and V4d was greater than this general bias. V4v shows a higher responsiveness to color than the adjoining V3v and a similar responsiveness to VO1. V4d shows lower color responsiveness than V3d and similar color responsiveness to LO. We believe that this result clearly demonstrates a functional difference between V4v and V4d, which strongly argues against their belonging to a single visual area.

Small asymmetries between the dorsal and ventral parts of V2 and V3 in their color responsiveness

Overall, V1, V2, and V3 showed a weaker color response than ventral V4 and VO. In area V2, the dorsal and ventral parts showed approximately the same color response, while in V3 the dorsal component showed greater color responsiveness than the ventral component, although the magnitude of this bias was smaller than that of the (opposite) bias of V4v to show greater color responsiveness than V4d.

In macaque V2, there are color-selective cells (for example, Hubel & Livingstone, 1987; Kiper, Fenstemaker, & Gegenfurtner, 1997) and maps of hue preference (Xiao, Wang, & Felleman, 2003). Using fMRI, Wade et al. (2008) found that the dorsal and ventral parts of macaque V2 showed similar color responsiveness, consistent with the general agreement that the ventral and dorsal parts of V2 form a single visual area in both macaque and human.

Color responsiveness in V3 has been less extensively investigated than color responsiveness in V4, but V3

shows a similar proportion of color-sensitive cells to V2 (Gegenfurtner, Kiper, & Levitt, 1997). In macaque, it has previously been reported that the ventral part of V3 (also called VP) responds to color more than the dorsal part (Burkhalter, Felleman, Newsome, & van Essen, 1986; Felleman & van Essen, 1987); the bias we found goes in the opposite direction.

Visual field coverage according to the two models of V4

One of the central arguments Hansen et al. (2007) proposed in favor of the V4d/V4v model of human V4 was that visual field coverage in ventral V4 excluded the lower vertical meridian and surrounding angles. We found that the ventral hemifield model of V4 was not as lacking in coverage of the visual field as Hansen et al. (2007) reported it to be, but for most subjects a more complete visual field coverage was provided by the split V4d/V4v model (see Figure 7).

The fact that we found any coverage of the lower vertical meridian in ventral V4 weakens the claim of Hansen et al. (2007), who report that this coverage is not found in the region surrounding V4v. V4d does tend to provide better visual field coverage than the extra region near V4v, but when we have already demonstrated a functional difference between these areas, the question becomes whether the coverage in area V4v is clearly deficient without recourse to inclusion of a dorsal part. We believe that it is not, and that the coverage of this extra part of V4v, while not as complete as V4d, is not clearly deficient. This view is supported by the findings of Winawer et al. (2010), who recently described BOLD signal artifacts in the region of the transverse sinus. Ventral human V4 is often situated around the transverse sinus (Winawer et al., 2010), which alone may account for a weaker, less coherent response in the region corresponding to the lower vertical meridian representation according to the ventral hemifield model.

Implications for homology between humans and non-human primates

If human V4 is a single ventral hemifield, this is a significant departure from the accepted model of V4 in macaque, where V4 is split into dorsal and ventral hemifield representations. To what extent should we expect homology between humans and non-human primates? Between primate species and within individuals of the same species, there is least variation for areas V1 and MT, which are specified early in development (Rosa & Tweedale, 2005). Progressing from V1 to V2, V3, and other areas, maps of the visual field become less clearly defined, and variability between individuals increases (Rosa & Tweedale, 2005). The notion that these areas are less clearly defined is consistent with the history of controversy regarding definitions of V3 and V4 in macaques, as described in the Introduction section. Functional differences between species are also more likely for later visual areas; for example, Wandell et al. (2007) note that while V3A is not especially responsive to motion in macaque, it is strongly responsive in humans.

Since V4 is a later visual area, it would be less surprising if there were a breakdown of the homology between macaque and humans in this area than in, say, V1 or V2. It is unclear how differences in retinotopic organization might be linked to differences in functional organization. The difference in retinotopic organization between macaques and humans may imply that there is also a difference in the functional role of V4, although the color responsiveness we found here is consistent with reports of V4 being of particular importance in color perception for macaques. Further work may reveal a functional difference between macaque V4 and human ventral hemifield V4, but current evidence is consistent with both areas being involved in form vision, and particularly concerned with color.

Conclusions

Hansen et al. (2007) argued that human V4 includes a dorsal component on the basis that dorsal V4 complements the otherwise deficient visual field coverage of ventral V4 and that dorsal and ventral V4 show similar attentional modulation. They also make the point that a model that is homologous with that accepted for non-human primates should be maintained until there is strong evidence to reject it. We have shown that while V4v shows a strong color responsiveness, V4d shows a weaker color responsiveness even than some surrounding areas. We believe that this functional difference in the responsiveness of V4v and V4d argues against their belonging to a single visual area and that visual field coverage in ventral V4 is not deficient enough to warrant maintenance of the split V4d/V4v model. Instead, we agree with previous suggestions that in humans V4 is composed of a single ventral hemifield representation.

Appendix A

Overall responsiveness across the visual cortex

In order to check that the differences in the color responsiveness of different areas could not be attributed to

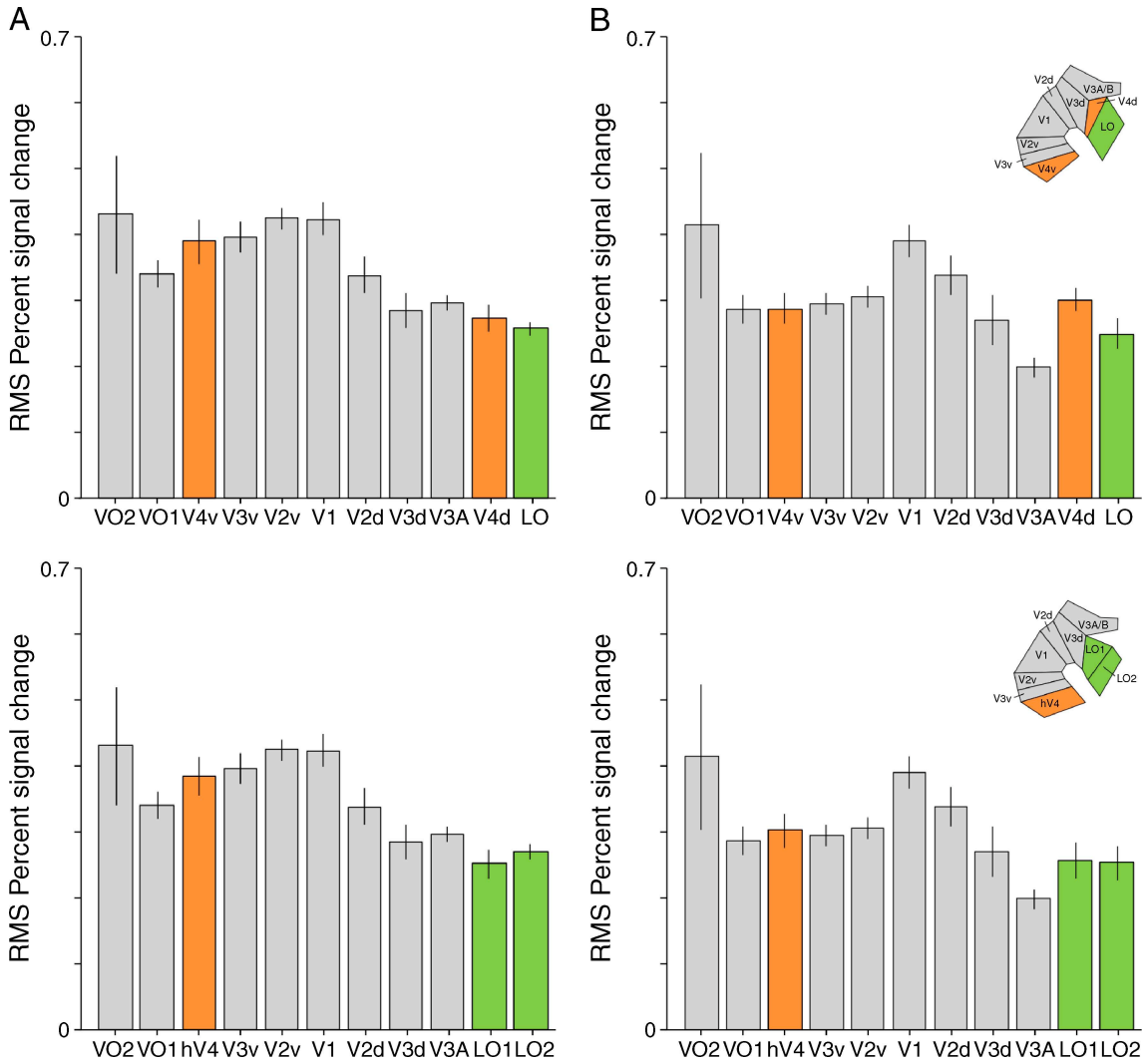

Figure A1. Variability in the BOLD response of each area, calculated as the RMS percent signal change in the BOLD for that area, using (A) all data or (B) only data from the achromatic blocks. Upper and lower barplots correspond to the two models of how V4 is organized, as in Figure 6.

differences in their overall responsiveness, we examined the variability in the BOLD response of each area. In Figure A1, we plot the RMS percent signal change, that is, the standard deviation of the BOLD signal divided by its mean.

When we included all the data in our analysis (Figure A1A), there was a tendency for ventral areas to show greater signal variability than dorsal areas. However, when we included data from only the achromatic blocks (excluding all color blocks and the first and last data images acquired during each achromatic block, plotted in Figure A1B), there was less of a tendency for ventral areas to show greater variability than dorsal areas. In particular, there was little if any difference between V4v and V4d when considering the achromatic blocks alone. This implies that the difference between V4v and V4d in Figure A1A most likely reflects variance introduced by the modulation of the response of V4v with the color/achromatic cycle of the stimulus. When this feature of the stimulus is removed by considering only data from the achromatic blocks (Figure A1B), V4d and V4v show very similar signal variability, implying that the differences in their color responsiveness cannot be attributed to V4d showing a lower signal irrespective of the stimulus.

Appendix B

Color responsiveness based on percent responding voxels

In addition to the analysis plotted in Figure 6, we performed a second analysis of the color responsiveness

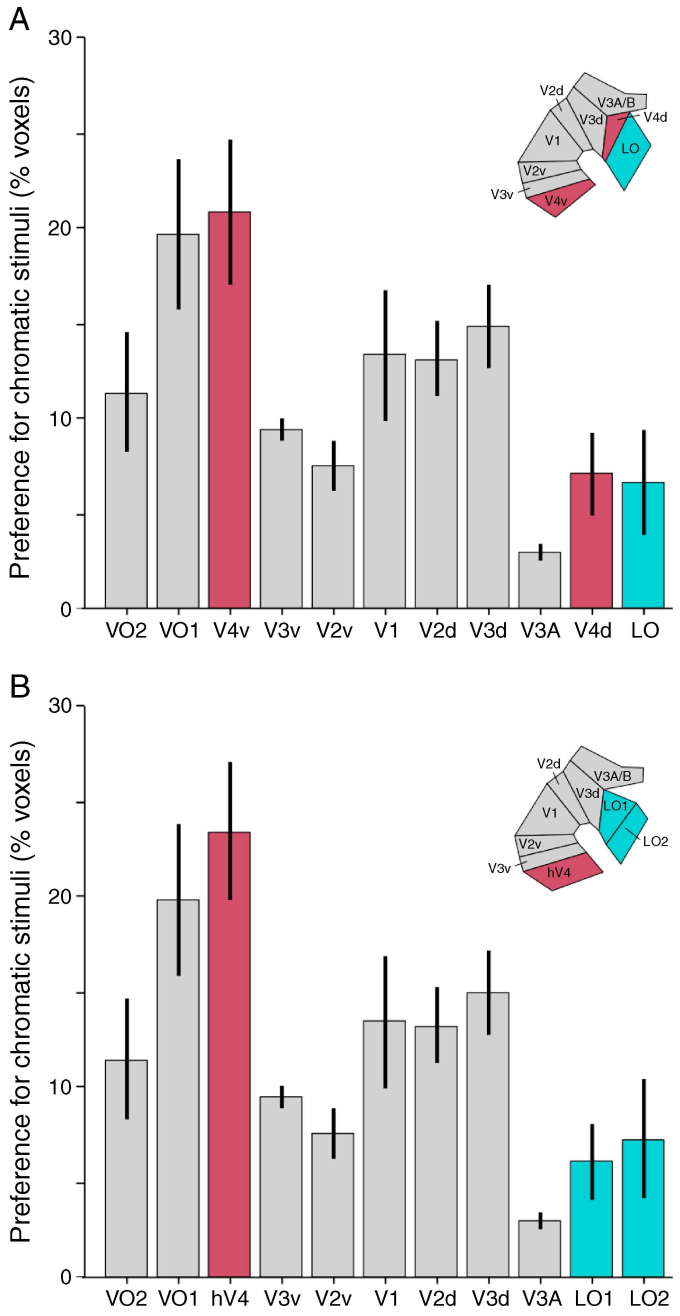

Figure B1. Color preference of each area, according to (A) the split dorsal/ventral model of V4 and (B) the ventral hemifield model of V4. The bars indicate the extent to which each area shows a reliable response modulation with stimulus color. Reported preference for chromatic stimuli is the percentage of voxels that show a reliable modulation (coherence > 1 *SD* above the individual's mean coherence) with stimulus color and a greater response to chromatic than achromatic blocks. Error bars show the mean ± 1 standard error of the between-subjects mean.

of each area, using the percentage of voxels that showed a reliable modulation with stimulus color as the dependent measure. The results of this analysis, plotted in Figure B1, were very similar to the results in the original analysis and offer additional support to the claim that V4v shows a clear preference for colored stimuli while V4d does not.

Appendix C

Color responsiveness with potential primacy effects removed

In our experimental design, each movie clip was seen by each subject in black and white and in color an equal number of times. However, if there were a primacy effect, where subjects showed an enhanced response to each type of block the first time it was viewed, this may have resulted in an artifact in our data.

Due to our experimental design, where half the blocks were seen first in color and half were seen first in black and white, any enhancement should be approximately balanced: the first viewing of odd numbered blocks will increase the overall response to color, while the first viewing of even numbered blocks will increase the overall response to the achromatic stimuli. However, if the odd and even blocks evoke different overall responses, a stronger response to the initial time each block is viewed would introduce an artifact in our data.

To test the possibility that this artifact affected our results, we repeated our analysis of color preference for just the last two runs of the data (those blocks outlined in a blue dashed line in Figure C1). The results of this analysis are plotted in Figure C2. We found that the main result was unchanged: using a paired two-tailed *t*-test to compare the normalized Fourier amplitude values for

Figure C1. Schematic illustrating the experimental design. Subjects each viewed 4 runs comprised of 18 blocks, each lasting 15 s. The movie clip that was looped lasted 2 min, giving 8 different block types (numbered 1 to 8 above). In each run, color blocks were interleaved with achromatic blocks, shown as red and gray, respectively, in the above schematic. The first viewings of each block type (when achromatic or in color), in the first 8 blocks of the first and second runs, are highlighted. Odd blocks were first viewed in color, while even blocks were first viewed in black and white. The solid green line surrounds the blocks that were included in our original analysis, and the dotted blue line indicates the blocks that were included in the supplementary analysis reported here.

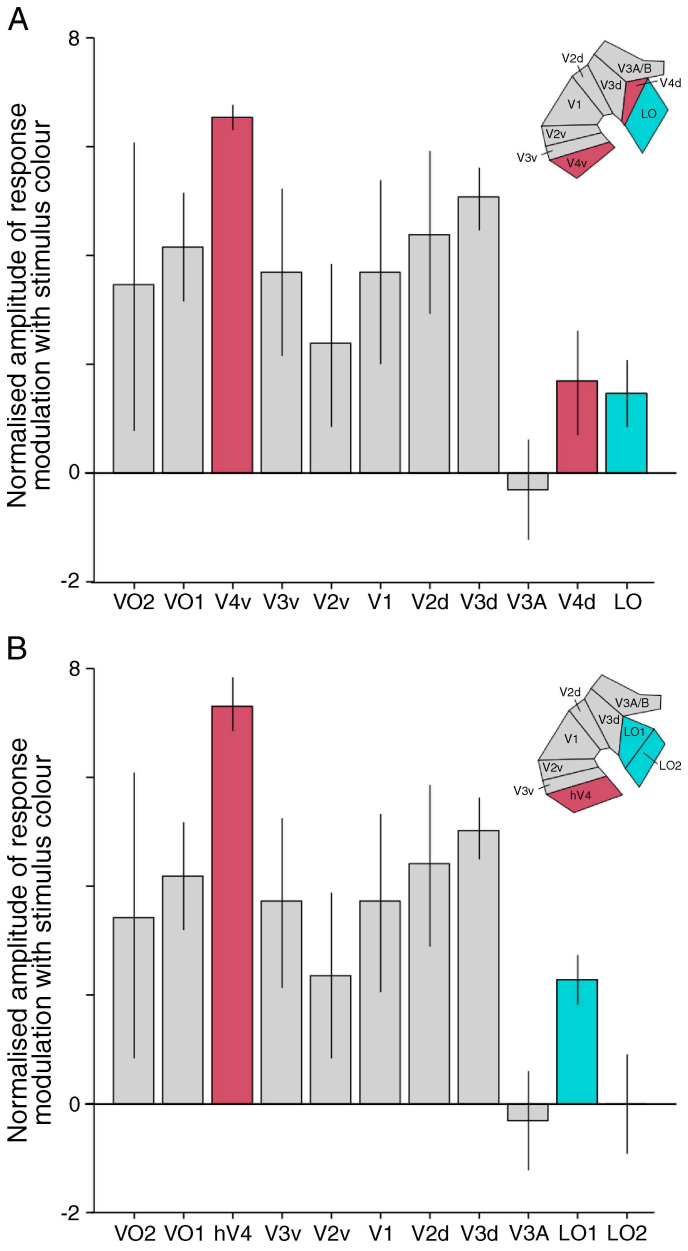

Figure C2. Color responsiveness of each area, according to (A) the split dorsal/ventral model of V4 and (B) the ventral hemifield model of V4, based on data from the third and fourth runs for each subject. Conventions as in Figure 6.

areas V4d and V4v, we found that the color responsiveness of V4v was significantly greater than V4d ($p < 0.01$, $t(5) = 4.18$).

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