

Combined orientation and colour information in human V1 for both L–M and S-cone chromatic axes

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Although it is widely held that colour and form are processed separately in early visual cortex, there is growing evidence that primary visual cortex (V1) may show some joint selectivity for orientation and colour. Colour is supplied to V1 via two very different pathways: the parvocellular pathway (which also supports detailed form processing) carries L–M (“red–green”) chromatic information, while a koniocellular pathway carries S-cone (“lilac–yellow”) information. Therefore on entering V1, S-cone information is segregated from the pathways carrying form information, while L–M information is not. Whether signals from neuronal populations in human V1 reflect combined orientation and S-cone information has not been systematically addressed. We used fMRI in combination with a multivariate data analysis technique to investigate whether BOLD signals recorded from V1 contain information that could directly discriminate between orientations based on different types of chromatic information. We found selectivity in V1 for L–M and luminance-defined orientation signals, and most interestingly, also for S-cone defined orientation. We also found similarly successful orientation discrimination for both colour dimensions in V2 and V3. These results imply that a proportion of cells throughout human visual cortex show joint sensitivity to both colour and orientation. We discuss also the potential role of feedback to V1 from higher visual areas.

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Introduction

It is widely believed that fundamental visual features, such as colour and orientation, are processed independently in human visual cortex. This pervasive concept has received support from a variety of sources. For example, neurophysiological studies of macaque primary and secondary visual cortex (V1 and V2) reported separate populations of colour-selective cells and orienta-

tion selective cells (DeYoe and Van Essen, 1985; Landisman and Ts'o, 2002; Lennie et al., 1990; Livingstone and Hubel, 1988; Livingstone and Hubel, 1984; Roe and Ts'o, 1999; Shipp and Zeki, 2002; Ts'o and Gilbert, 1988). Patients with damage around V4 showed dramatic colour vision deficits without much apparent loss of form perception (Meadows, 1974; Zeki, 1990), while fMRI studies found “colour-specific” activity in approximately the same area (Lueck et al., 1989; McKeefry and Zeki, 1997). Many perceptual and behavioural observations are also consistent with separate processing of colour and form (Holmes et al., 2006; Livingstone and Hubel, 1987). Thus the idea of segregated feature processing has been widely accepted, although it remained unclear how the information is combined into a unified percept.

However, the data supporting segregated feature processing have become increasingly controversial, and there is growing evidence for considerable overlap in colour and orientation representations in monkey and human visual cortex (Friedman et al., 2003; Gegenfurtner, 2003; Leventhal et al., 1995; Thorell et al., 1984). For example, there are behavioural examples of colour orientation contingency (e.g., McCollough, 1965), and careful examination of lesion cases in humans or macaques reveals no clear case of colour impairment in the absence of any impairment to form processing (e.g., Gallant et al., 2000). Likewise, fMRI studies find no region that can be activated only by colour (e.g., Chelazzi et al., 2001), while V1 and V2 reflect colour contrast adaptation that is orientation specific (as well as colour adaptation that is not orientation specific) (Engel, 2005). Similarly, in macaque V1 and V2, in addition to colour cells that are not orientation selective, several studies have reported cells that code both orientation and colour to some degree (Friedman et al., 2003; Gegenfurtner, 2003; Leventhal et al., 1995), and despite controversy in interpretation, the relative numbers of such cells found do not differ dramatically across studies (Schluppeck and Engel, 2002). Thus it may be that colour and form information are never fully segregated.

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Colour information is supplied to V1 by two very different geniculostriate pathways. Chromatic comparison of signals from long-wave-sensitive (L) and medium-wave-sensitive (M) cones is carried by the parvocellular pathway, which also supplies detailed form information via small centre-surround receptive fields. This pathway is thought to have existed in ancestral primates before the divergence of primate L and M cone pigments (Ghosh et al., 1996; O'Keefe et al., 1998; Yamada et al., 1998, 1996). Colour information travelling in this pathway could thus be considered “parasitic” on a pre-existing mechanism for conveying form information (Mollon, 1989). From this perspective, since orientation selective neuronal populations in V1 draw parvocellular input, it would not be surprising if chromatic L–M information was always present in the same population of cells. Indeed, it would seem computationally more complex to entirely segregate the features, only to combine them again later for object recognition.

Chromatic information from short-wave (S) cones, on the other hand, is supplied to V1 by afferents from koniocellular layers of the LGN. This pathway provides colour opponent comparison of S-cone signals with pooled L and M cone signals and projects to layers 3B and 4A of V1 (Chatterjee and Callaway, 2003). It is therefore segregated from the parvocellular L–M afferents, which project to layer 4C β (Chatterjee and Callaway, 2003). The S-cone pathway has large non-spatially opponent receptive fields (e.g., Dacey and Packer, 2003) and low spatial resolution (Cavonius and Estevez, 1975). Perceptual observations indicate that S-cone form information is not strong and is generally overridden by luminance or L–M form information (e.g., West et al., 1996). For example, if a curved luminance edge is superimposed on a straight S-cone chromatic edge, the latter can appear aligned with the curved luminance edge. Since S-cone chromatic information enters V1 by a channel distinct from the L–M channel, it is plausible that any orientation information it contains may be extracted at a different stage.

There are little neurophysiological data and no human fMRI data concerning whether signals reflecting S-cone orientation information can be observed in V1. There is evidence that many V1 colour cells receive both L–M and S-cone information (De Valois et al., 2000; Landisman and Ts'o, 2002) and that some of these cells also code orientation (Friedman et al., 2003; Leventhal et al., 1995). But it remains possible that any orientation selectivity may have been derived only from the inputs carrying the L–M information, and the S-cone information may be entirely unoriented. The most specific data on the question of combined colour and form representation in V1 hint at much less form selectivity for S-cone information than for L–M information (Johnson et al., 2001).

Here we used high field BOLD contrast fMRI to investigate whether human retinotopic areas V1–V3 contain combined chromaticity and orientation information for both L–M chromaticity and S-cone chromaticity. We tested whether fine-grained spatial patterns of activity within these areas could discriminate between differently oriented gratings defined only by chromatic information. Different orientations and colours are represented at a much finer spatial scale than the spatial resolution of conventional fMRI, and therefore the BOLD signal from a region of interest, or even a single voxel, will not on average distinguish between stimuli that differ only in orientation. However, recent work shows that the fine-grained spatial pattern of BOLD signals in retinotopic areas V1–V3 contains information sufficient to allow above-chance discrimination between differently oriented luminance (black–white) gratings using multivariate pattern-based decoding (Haynes and Rees, 2005a; Kamitani and Tong, 2005). Despite the low resolution of fMRI compared to orientation columns in V1, multivariate techniques may be successful because anisotropic distribution of these columns can lead to slight but reliable orientation biases in many fMRI voxels (Haynes and Rees, 2005a, 2006; Kamitani and Tong, 2005, other explanations are considered below).

Multivariate pattern recognition approaches can successfully classify various visual properties in areas already known to code these properties: e.g., orientation in V1, V2 and V3 (Haynes and Rees, 2005a; Kamitani and Tong, 2005), motion direction in V5 (Kamitani and Tong, 2006), faces and objects in IT (Haxby et al., 2001; O'Toole et al., 2005) and attentional allocation in V1 and V5 (Kamitani and Tong, 2005, 2006). Here we go beyond this important earlier work that has proved the sensitivity of the multivariate approach by using it to test an unresolved physiological question concerning the properties of human visual cortex. We hypothesized that, for brain regions containing combined chromatic and orientation information, it should be possible to use the pattern of fMRI signals across voxels to discriminate between chromatically defined orientations because the distribution of neuronal activity will be different for each stimulus. Conversely, if colour and orientation information is carried mainly by different neuronal populations, differently oriented chromatic stimuli would simply activate the same population of chromatic cells, creating no consistent differences in voxel biases and thus not allowing successful discrimination.

We measured brain activity in retinotopic visual cortex of adult humans viewing luminance gratings, L–M (pinkish-green) gratings or S-cone (lilac–yellow/green) chromatic gratings (Fig. 1). Importantly, the chromatic stimuli were psychophysically cali-

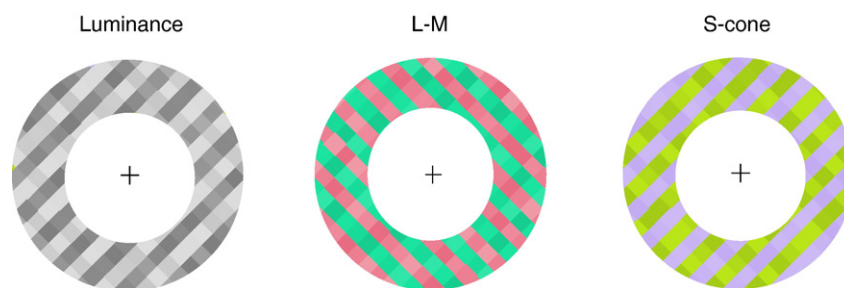


Fig. 1. Schematic illustration of luminance, L–M and S-cone stimuli. The gratings reversed every 133 ms (so that, for example, red stripes became green and vice versa) and changed orientation from 45° to –45°, or vice versa, every 20 s, with brief pauses (2.6 s) between blocks. Note that each square had a random luminance between limits to create dynamic luminance noise (the colours depicted can only be representative, due to differences between different printers and monitors; furthermore, exact colours were calibrated individually for each participant).

brated for each participant in the scanner (Smithson et al., 2003; Sumner et al., 2002, 2006, 2004). Multivariate pattern classification was used to predict orientation for each type of stimulus from distributed response patterns in V1–V3, which were defined for each participant using standard cortical flattening and meridian mapping (Teo et al., 1997; Tootell et al., 1995; Wandell et al., 2000); see Fig. S1). Fig. 2 illustrates the methodological stages. Above-chance classification would mean that there was a consistently different pattern of signals associated with each orientation. We compared such multivariate classification performance with the results obtained from conventional univariate ('region of interest') analyses where the BOLD signal was simply averaged for each condition across stimulus responsive voxels, ignoring any fine-grained spatial pattern.

Materials and methods

Participants

Six volunteers (aged 24–32 years, 3 female) gave written informed consent to participate in the study, which was approved by the Institute of Neurology and National Hospital for Neurology and Neurosurgery Joint Ethics Committee. All had normal colour vision and normal or corrected to normal visual acuity.

Procedure

Following psychophysical calibration of the stimuli for each participant (see below), we measured the BOLD response while participants viewed luminance, L–M or S-cone gratings (Fig. 1). Each participant underwent six 7-minute fMRI sessions in a different palindromic order. In each session participants passively viewed a fixation cross during alternating blocks of 45° and –45° oriented gratings. In two sessions the gratings were defined by luminance, in two they were L–M chromatic gratings, and in two they were S-cone chromatic gratings. Each block was approximately 20 s long (16 fMRI volume acquisitions at TR 1.3s) with brief pauses (2 volumes, 2.6 s) between blocks. There were 16 blocks per session.

Stimuli

The stimuli were gratings oriented at either 45° or –45° which changed orientation every 20 s. These were composed of a

chequerboard of square patches tilted at 45° and windowed by an annulus subtending 6° to 12° (Fig. 1). 45° or –45° oriented gratings were created by shifting the mean chromaticity or luminance of the squares in alternative orthogonal striped patterns. Each square was 0.6° across, so the fundamental spatial frequency of the grating was 0.8 cpd. The gratings were in 3.75 Hz counterphase. For example, in the case of luminance gratings, every 133 ms the light stripes became dark stripes and vice versa. At each phase reversal each square was independently assigned a random luminance level within a range of 2 cdm⁻² around the currently assigned mean value for that square. This created dynamic luminance noise that would prevent the edges of the chromatic stripes being visible to luminance channels (note that equiluminance does not hide chromatic edges from the magnocellular pathway, Birch et al., 1992; Logothetis et al., 1989; Mollon, 1982).

The background was grey (MacLeod-Boynton colour coordinates, MB, 0.65, 0.02; luminance, 15 cdm⁻²) with a white fixation cross (50 cdm⁻²) at the centre of the annulus. The mean chromaticity of the annulus was the same grey, and the mean luminance was 25 cdm⁻². For the luminance stimuli, the luminance of the light and dark stripes were incremented or decremented by 5 cdm⁻² (20%), respectively (additive with the luminance noise).

S-cone stimuli are colour transitions that leave unchanged the signals of long-wave (L)- and middle-wave (M)-sensitive cones, while affecting the signal in short-wave cones. Our transitions were from lilac to yellow/green, being approximately plus and minus 80% S-cone contrast from the chosen neutral grey chromaticity (because the S-cone system is approximately 4 times less sensitive than the luminance system, Wyszecki and Stiles, 1982). The exact colour transitions that do not affect L and M cones differ between individuals, and between retinal locations, because of variations in cone sensitivity, macular pigment, lens optical density and chromatic aberration. Therefore the S-cone stimuli were calibrated individually for each participant while they were in the scanner, using procedures similar to those previously described, employing transient tritanopia plus the minimum motion technique for equiluminance (Anstis and Cavanagh, 1983; Smithson et al., 2003; Sumner et al., 2002, 2006, 2004). Note that the use of an annulus stimulus avoided the central retinal area where the S-cone chromatic axis changes most owing to changing macular pigment density.

For the L–M chromatic stimuli, the chromaticity of the squares was incremented or decremented by 20% along the theoretical

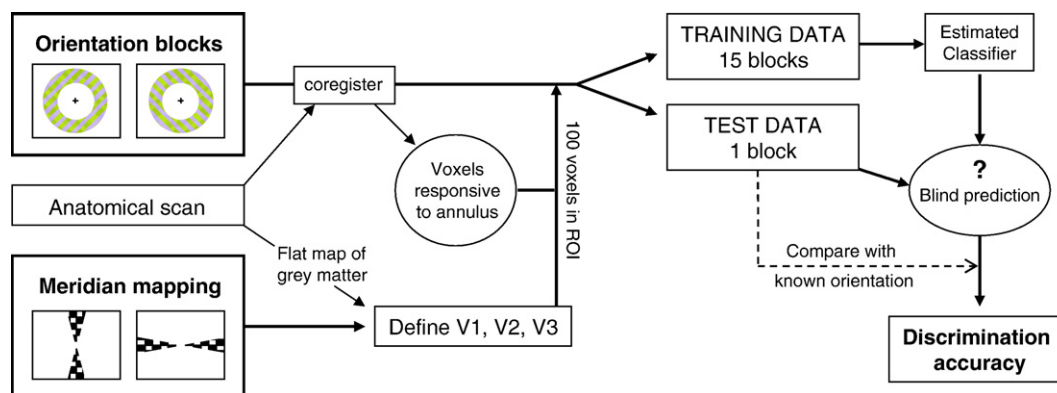


Fig. 2. Schematic illustration of methodological steps. See Materials and methods for more details and Fig. S1 for an example of meridian mapping and selection of stimulus-responsive voxels.

L–M chromatic axis (pinkish red to green-turquoise). The appropriate luminance for each colour was calibrated for each participant as for the S-cone stimuli.

All stimuli were created and presented using a PC-controlled Cambridge Research Systems (CRS) ViSaGe directly connected to an LCD projector NEC LT158, projecting onto a screen at the back of the magnet bore. Stimulus presentation was synchronised with the screen refresh rate of 60 Hz, and the beginning of each block was triggered by the MR acquisition cycle. Fixation was monitored using an Applied Science Laboratories MR-compatible remote infrared eye-tracker (ASL540LRO).

fMRI acquisition

Functional MR images were acquired on a Siemens Allegra 3 T scanner with standard head coil. Six sessions of 298 volumes were acquired per participant in the main experiment (in palindromic counterbalanced orders), at a conventional resolution of $3 \times 3 \times 3$ mm. Each volume had 20 slices and a TR of 1.3 s. Following 10 initial volumes to allow for magnetic saturation, each block of each orientation comprised 16 volumes with the stimulus present and 2 volumes with only the fixation cross. MR acquisition in the control experiment was identical, except that there were 4 sessions per participant instead of 6.

Functional masks

To identify visually responsive voxels to be used in the pattern classification, in appropriate retinotopic regions for our annulus stimuli, functional masks were obtained for each kind of stimulus (luminance, L–M or S-cone) for each participant. The first 10 volumes of each session were discarded and the remainder were realigned, resliced and coregistered to the same structural image used for that participant's retinotopy (using SPM2, <http://www.fil.ion.ucl.ac.uk/spm>). The data were then modelled voxel-wise using a standard general linear model as employed by SPM2 (Friston et al., 1995). F-contrast masks were produced incorporating activity from either orientation and thresholded so that there were at least 100 voxels per region (V1, V2 or V3) per participant.

Pattern classification

Based on the protocols for multivariate analysis outlined previously (Haynes and Rees, 2005a), we extracted, for each participant, the raw BOLD signal from 100 voxels in each of V1, V2 and V3 for either luminance, L–M or S-cone gratings. The voxels were selected using the functional masks described above, so that they came from appropriate retinotopic regions responsive to the annulus stimuli (see Fig. 2 and S1). One part of the data was used to train a multivariate pattern classifier to distinguish between the activity patterns for each orientation. Based on this training, the classifier then attempted to blindly classify the orientations represented in the other, independent, part of the data (the “test”). This was repeated for different allocations of the data to training and test, and mean classification accuracy was obtained for that stimulus (luminance, L–M or S-cone) for that area (V1, V2 or V3) for that participant.

The first 4 volumes of each block were discarded to allow the delayed BOLD signal to approach stability. The remaining 12 images from 15 of the blocks for each orientation were assigned to a *training* data set (a total of 360 volumes), while the remaining

24 images (the images from the remaining block for each orientation) were assigned to be the *test* data set. Classification performance was assessed using linear discriminant analysis with *m*-fold cross-validation (Duda et al., 2001). Note that training and test data sets were from independent blocks and that we used the raw fMRI signal in the coregistered images (the general linear model was used only for identifying the voxels to be included in the analysis, as described above). This cycle was repeated 16 times using different blocks for training and test, and mean accuracy calculated over these 16 cycles. See Fig. 2 for schematic of methodological stages and Supplementary material for more details.

Retinotopy

Following the main experiment, we acquired for each participant a T1-weighted structural image and two functional runs of 165 volumes each for the purposes of defining areas V1, V2 and V3 using standard cortical flattening and meridian mapping procedures (Teo et al., 1997; Tootell et al., 1995; Wandell et al., 2000). Participants viewed standard high contrast reversing chequerboard (8Hz) stimuli that stimulated either the horizontal or vertical meridians. V1, V2 and V3 were identified in each participant using segmentation and cortical flattening in MrGray (Teo et al., 1997; Wandell et al., 2000) using standard definitions for the borders between regions (Serenio et al., 1995; Tootell et al., 1995). See Fig. S1.

Control experiment

A difficulty for chromatic stimuli in the MRI environment is presented by the use of LCD projectors, which produce much poorer spatial uniformity across the stimulus than do the CRT monitors traditionally used in colour psychophysics. The main non-uniformity is in overall luminance of the projected image, which would not create luminance artefact in our chromatic stimuli because both colours in the stimulus would be equally modulated in luminance. However, there is generally also some slight non-uniformity in colour balance, and this could produce luminance differences between the different colours in our chromatic gratings, which could, in theory, provide some luminance orientation information that was not completely disguised by the luminance noise. A similar issue is created by possible inhomogeneous retinal sensitivity across the extent of the stimuli (though note that the annuli lay outside the macular region over which wavelength sensitivity differs most).

Therefore, in a control experiment we measured the upper discrimination limit obtainable from any possible luminance artefact in the chromatic stimuli to test whether results for the S-cone stimuli could be explained by luminance artefacts in the stimuli. For two participants, we measured equiluminance points for the chromatic stimuli, in the scanner, at several locations around the annulus, using the technique of minimum motion (Anstis and Cavanagh, 1983). For S-cone stimuli we found maximum deviations of 1.2 and 1.0 cdm^{-2} from mean settings, and the deviation in L–M equiluminance was smaller. We then performed further fMRI sessions using luminance stimuli with a contrast equal to this maximum deviation (and the same luminance noise range as in the main experiment: 2 cdm^{-2}). Note that these control luminance gratings had this contrast across the whole stimulus, whereas the S-cone stimuli had it only in patches of the stimulus.

Thus the control luminance stimuli overestimated the degree of luminance artefact in the S-cone stimuli, setting an upper limit on the discrimination performance that might result from such artefact. We also performed further S-cone fMRI sessions using the mean equiluminance setting obtained. Therefore the two participants underwent four additional sessions, two with low luminance contrast stimuli and two with S-cone stimuli, in a counterbalanced palindromic order.

Results

Univariate analysis

As expected, univariate analysis, in which BOLD signal was averaged across stimulus-responsive voxels in each ROI (V1–V3), failed to discriminate between orientations for luminance or chromatic stimuli in any ROI: the difference between the mean BOLD signals for each orientation (using the same voxels used in the multivariate analyses below) was always less than 0.02% for each stimulus type in each ROI. We also examined the activity in each quadrant of V1 (left and right, dorsal and ventral) for each orientation to discover if radially oriented stripes produced greater activity than tangential stripes (Sasaki et al., 2006). For luminance stimuli, we found a hint of such a global bias, which although very small (0.0027%) was consistent in direction across subjects ($t_{(5)}=3.0$, $p=0.03$). However, for chromatic stimuli there was no evidence of a consistent bias whatsoever: mean bias for L–M stimuli was 0.0003% ($t_{(5)}=0.01$, $p=0.99$), while mean bias for S-cone stimuli was -0.0009% ($t_{(5)}=0.3$, $p=0.81$).

Luminance stimuli

The discrimination accuracy for orientation defined by luminance, based on the activity pattern in V1 voxels responsive to our annulus stimuli (see Materials and methods), was between 60% and 85% in all participants, with a mean of 68.8% (Fig. 3A). This was significantly above-chance performance of 50% ($t_{(5)}=5.4$, $p<0.01$). Similar discrimination accuracies were obtained for V2 and V3, with means of 68.4% and 65.1%, respectively ($t_{(5)}=3.9$, $p<0.01$; $t_{(5)}=3.7$, $p<0.01$). The apparent slight trend of decreasing accuracy from V1 to V3 (see Fig. 3A) was not statistically significant ($F_{(2,10)}=1.7$).

L–M chromatic stimuli

Orientation based on L–M chromaticity was also successfully discriminated by the activity pattern in stimulus-responsive V1 voxels (Fig. 3B). Mean discrimination was 61.7%, ranging between 57% and 66.7% across participants, which was significantly above-chance performance ($t_{(5)}=7.8$, $p<0.001$). Similarly successful discrimination was obtained for V2 (61.9%, $t_{(5)}=4.1$, $p<0.01$) and V3 (64.4%, $t_{(5)}=4.2$, $p<0.01$), with no significant difference between regions ($F_{(2,10)}=1.2$).

S-cone chromatic stimuli

Most interestingly, the activity pattern in stimulus-responsive V1 voxels also successfully discriminated the orientation of S-cone stimuli (Fig. 3C). The mean accuracy level was 62%, which was significantly above chance ($t_{(5)}=8.5$, $p<0.001$). Results for

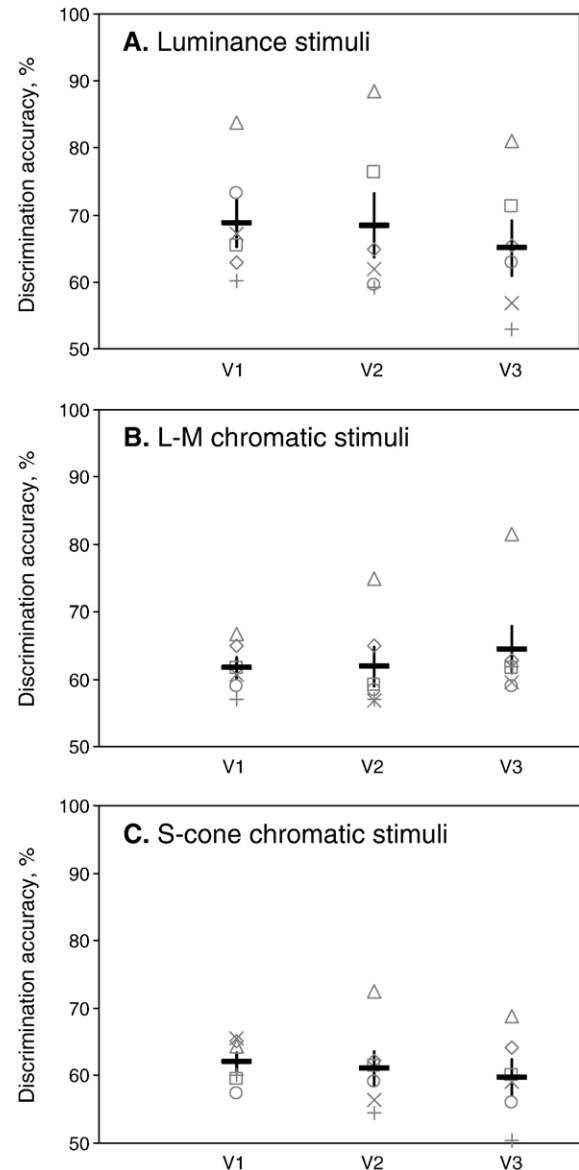


Fig. 3. Orientation discrimination accuracy. (A) Discrimination results for luminance-defined orientation based on patterns of fMRI signal across 100 voxels in each of V1, V2 and V3. The solid bar shows mean discrimination accuracy across participants (error bars are standard error). Light symbols represent mean accuracy for individual participants. (B) Discrimination results for orientation defined by L–M (‘red–green’) chromaticity, based on patterns of fMRI signal across 100 voxels in each of V1, V2 and V3 (symbols as for A). (C) Discrimination results for orientation defined by S-cone chromaticity (‘lilac–yellow’), based on patterns of fMRI signal across 100 voxels in each of V1, V2 and V3 (symbols as for A).

individual participants ranged between 57.4% and 65.6% and are shown in more detail in Fig. S2. Voxels in V2 produced successful discrimination at a similar level (61%, $t_{(5)}=4.3$, $p<0.01$), as did voxels in V3 (60%, $t_{(5)}=3.7$, $p<0.01$). Again there was no significant difference between regions ($F_{(2,10)}=0.6$). As a control, we repeated the analysis for V1 with voxels that were not stimulus-responsive (i.e., not in the retinotopic region activated by the annulus stimuli, see Fig. S1). As expected, orientation discrimination failed for these voxels (mean accuracy < 50%).

Specificity

The results reported above show that signals in human V1 can discriminate between orientations coded by colour, but do not precisely constrain the nature of the underlying neuronal representations associated with such signals. For example, it is conceivable that colour-defined orientation is determined in higher cortical areas and then fed back to neuronal populations in early visual cortex selective for orientation but not colour. However, if this were the case then it should be possible to train a classifier on L–M stimuli and successfully test on S-cone stimuli (or vice versa) because the same population of neurons would be providing the orientation signals in V1 regardless of stimulus colour. However, our data do not support this possibility. Mean accuracy for training with L–M stimuli and testing with S-cone stimuli, or vice versa, was close to chance (52%). In contrast, when the same coloured stimuli were used for train and test mean accuracy was significantly higher ($t_{(5)}=6.4$, $p<0.01$) at 58% (Fig. 4). In both cases, for fair comparison, test and training data sets came from different fMRI sessions, which would explain why this mean accuracy value for within-colour conditions was lower than the values reported above — any head movements between sessions, for example, would act to reduce voxel-based pattern discrimination (see Fig. S6 in Haynes and Rees, 2005b). For V2 and V3 discrimination accuracy was also greater within-colour than between colour ($t_{(5)}=2.3$, $p<0.05$; $t_{(5)}=3.3$, $p<0.05$), again suggesting that orientation discrimination is largely based on underlying neuronal populations that contain combined orientation and colour information rather than based on populations that code orientation in a non-colour-specific manner.

To further test this conclusion, we tested discrimination accuracy in V1 when training on luminance stimuli and testing with chromatic stimuli or vice versa (train on chromatic stimuli and test on luminance). For luminance and S-cone stimuli, accuracy was 52.9%, while with luminance and L–M stimuli, accuracy was 54.7%. Both of these values fell short of the within-colour accuracies measured above, of 58.1% for S-cone and 58.3% for L–M (t -test comparisons of within-colour vs colour luminance

confirmed that these were significantly different: S-cone, $t_{(5)}=2.8$, $p<0.05$; L–M, $t_{(5)}=3.1$, $p<0.05$).

Additionally, we tested whether, when training and testing on the same colour, voxels most activated by the colour stimuli themselves, or by the luminance orientation stimuli, would provide most information about orientation. If colour-based orientation discrimination in V1 actually relies on information in non-colour-selective (“luminance”) cells that are activated, for example, by feedback from higher visual areas where colour-defined orientation is calculated, then the most useful voxels for orientation discrimination in V1 should be those activated by the oriented luminance stimuli. Under this hypothesis, the main activity produced by the colour stimuli would be in non-oriented colour cells, which are not useful for orientation discrimination, and any activated cells that were useful for orientation discrimination would also be activated by the luminance stimuli. Thus using voxels activated by the luminance stimuli should produce at least as good orientation discrimination for colour stimuli as produced by the voxels activated by the colour stimuli themselves. On the other hand, if colour-defined orientation discrimination relies on populations with combined orientation and colour information, it would be better to select voxels activated by stimuli of that colour. The latter prediction proved to be the case: orientation discrimination accuracy using voxels activated by the luminance stimuli was 55% for L–M stimuli and 57% for S-cone stimuli, whereas using the voxels activated by the coloured stimuli themselves, these values were both 62% ($t_{(5)}=11$, $p<0.001$; $t_{(5)}=2.7$, $p<0.05$). Similar patterns were evident also for V2 (58% and 57% vs 62% and 61%) and V3 (57% and 55% vs 64% and 60%).

Informative voxels

We investigated whether the voxels supplying the most information for orientation discrimination were positioned in any particular pattern with respect to the overall activity created by the stimuli and with respect to the retinotopic layout of early visual cortex. First, we assessed whether there was any correlation across voxels between the mean signal strength (in response to the annulus in either orientation) and the magnitude of the t -contrast between orientation conditions (i.e., a measure of the usefulness of this voxel for discrimination). Note that this was done only for voxels already selected by the functional mask, so by definition they were activated by the stimulus to some degree. A negative correlation might be expected, for example, if the most informative voxels were at the edge of the stimuli because these voxels tend to have weaker overall signal than those fully within the area activated by the stimulus (see Fig. S1B). However we found no correlation for any of our conditions (S-cone, L–M or luminance) for any participant, and neither was there any pattern in the values of the correlation coefficients across participants (i.e., the two numerically largest correlation coefficients were of opposite sign). Thus, amongst the voxels actually stimulated by the annuli, there appears to be no relationship between the overall level of this stimulation and the usefulness of this voxel for orientation discrimination.

Secondly, we plotted the positions of the voxels used in the orientation discrimination on flatmap representations of retinotopic visual cortex (Fig. 5 and Fig. S3). There was no discernable relationship between the locations of these voxels and how informative they were for orientation discrimination (represented

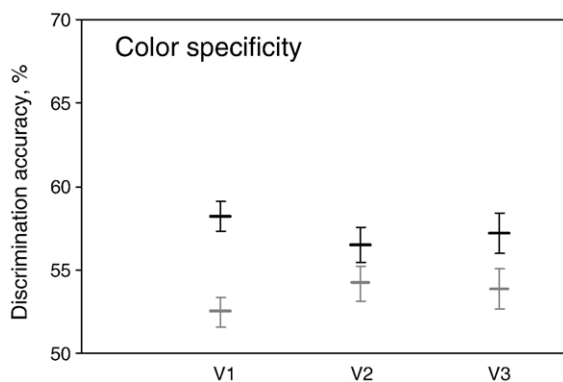


Fig. 4. Colour specificity of orientation discrimination. Black lines show mean discrimination accuracy (%) when training and test data sets used the same coloured stimuli (S-cone or L–M). Grey lines show mean discrimination accuracy (%) when S-cone stimuli were used for training and L–M for testing or vice versa (employing voxels activated by either coloured stimuli). Error bars are standard errors of the within subject difference between conditions (within colour vs between colour).

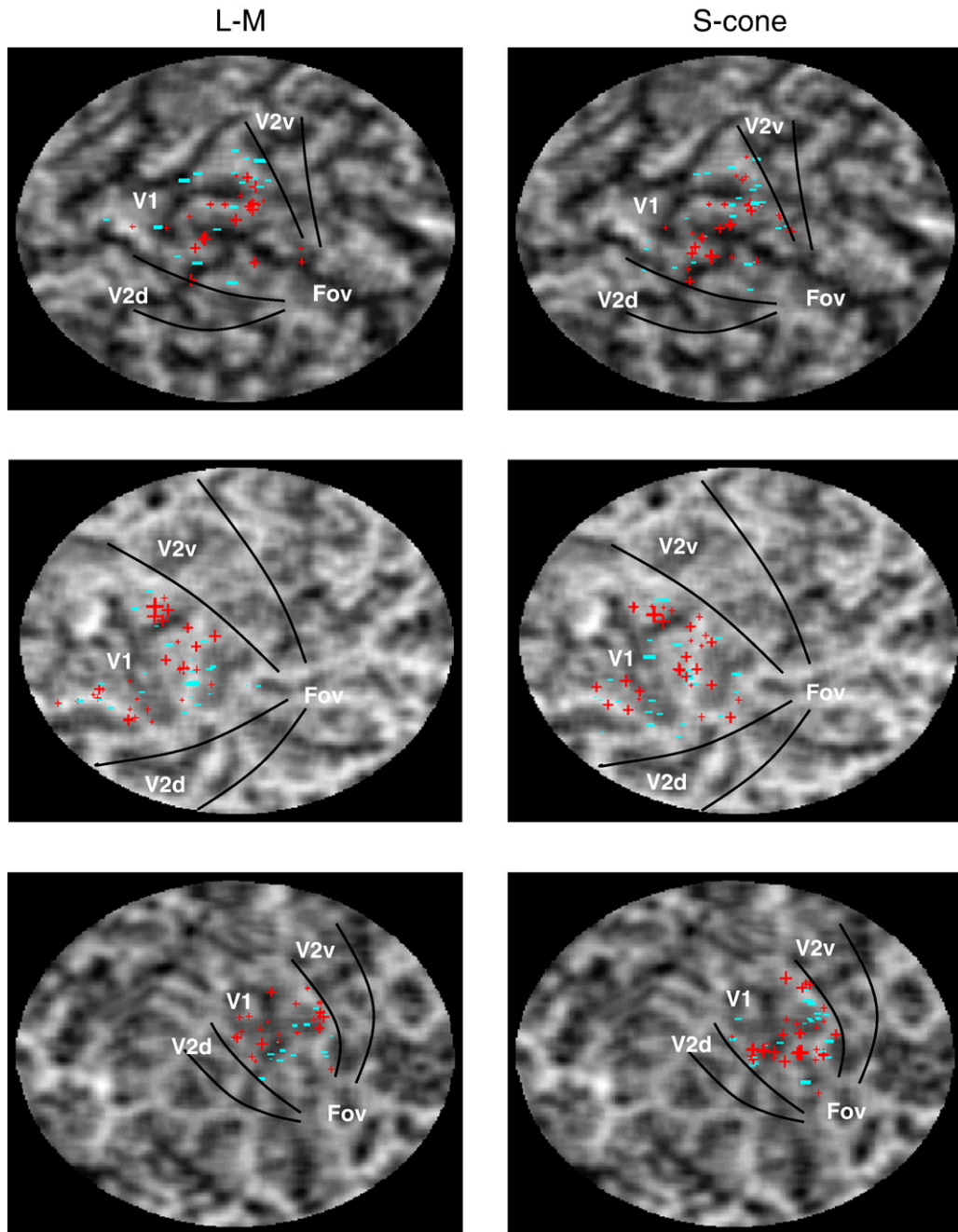


Fig. 5. Informative voxels in left V1 for orientation discrimination of chromatic stimuli. The positions of voxels used for orientation discrimination are plotted on flatmaps of left V1 for three participants (the three with the highest level of discrimination performance). The left column is for voxels used for the L–M stimuli, and the right column is for S-cone stimuli. For each voxel, the value of the t -contrast between orientation conditions (i.e., the usefulness of this voxel for orientation discrimination) is represented by the size of the symbol. Preference for the leftward orientation is depicted by a red plus sign, and preference for rightward orientation is depicted with a blue minus sign. There appears to be no consistent pattern in the arrangement of the informative voxels. The boundaries between visual areas were plotted as in Fig. S1, using meridian mapping (and the top two plots here are for the participant shown in Fig. S1). All voxels plotted were extracted from V1; the boundaries of V2 are shown to help orientation. (Note that cortical space is not represented linearly in flatmaps so that voxels that are equally far apart in V1 might either cluster very closely on the flatmap or be spread farther apart. Thus apparent gaps appear in the maps where voxels cannot be, or are very unlikely to be, plotted because these areas represent very small areas of cortex.) Further examples of right V1 for the crucial S-cone condition are shown in Fig. S3.

by the size of the symbols in Fig. 5 and Fig. S3). It is clear, for example, that the most informative voxels do not always cluster at the foveal or peripheral edges of the retinotopic representation activated by the stimulus. Haynes and Rees (2005a,b; Fig. S2)

also reported that informative voxels for luminance-defined orientation discrimination showed no systematic relationship to particular locations within the area of cortex activated by their stimuli.

Control experiment

In a second experiment we used control luminance stimuli to measure the upper limit of discrimination performance that might have been caused by luminance artefacts in the chromatic stimuli and compared it to new measurements of discrimination accuracy for S-cone stimuli. In V1, discrimination accuracy was 68.2% and 66.8% for the S-cone stimuli in each participant, but only 55.8% and 56.6% for the control luminance stimuli (Fig. 6). Given that the orientation of the control luminance stimuli was visible to the participants, it is not surprising that scotopic achromatopsia discrimination was possible based on them, but crucially, discrimination performance (i.e., difference from 50%) was 2–3 times higher for the S-cone stimuli ($t_{(15)}=2.5$, $p<0.01$; $t_{(15)}=2.3$, $p<0.05$). As shown, a similar pattern of results was produced by V2 ($t_{(15)}=3.7$, $p<0.01$; $t_{(15)}=2.8$, $p<0.01$) and V3 ($t_{(15)}=2.3$, $p<0.05$; $t_{(15)}=0.8$, $p>0.05$). This indicates that our observations of successful discrimination of S-cone stimuli in V1–V3 cannot be accounted for by luminance artefacts in the chromatic stimuli.

Discussion

We investigated whether the spatial pattern of BOLD signals across stimulus-responsive voxels in V1, V2 or V3 could discriminate between stimulus orientations defined by luminance, by L–M chromaticity or by S-cone chromaticity. In summary, we found that discrimination was successful for all three areas of visual cortex for all three types of stimulus. This is especially interesting in the case of S-cone stimuli, as discussed below. Discrimination of the chromatically defined orientations was specific to each colour and could not be explained by luminance artefacts in the stimuli.

Decoding orientation in V1–V3

Previous studies have reported successful multivariate prediction of orientation using luminance-defined gratings (Haynes and Rees, 2005a; Kamitani and Tong, 2005), and our findings for luminance-defined oriented stimuli are fully consistent with these earlier results. Previous work studied only high contrast (black–white) gratings, whereas we employed much lower contrast gratings embedded in luminance noise. As a consequence

prediction accuracy was generally lower for our stimuli (but still significantly above chance for all participants). Interestingly, however, there was little difference between the studies for the discrimination possible from V3 activity, implying that this area may be less influenced by physical stimulus properties than V1 and V2 and perhaps more influenced by the perceptual presence or absence of certain features. Such a difference in response properties between V3 and V1 would be consistent with the previous observation that V1 discriminated between masked orientations that were perceptually non-discriminable for the participant, while V3 did not (Haynes and Rees, 2005a).

The nature of the fMRI signals that allow successful multivariate discrimination remains debated. The simplest possibility would be differences in global activity between quadrants of the visual field, arising because radially oriented patterns can produce greater activity than tangential orientations (Sasaki et al., 2006). In this case, the neuronal populations would still be showing orientation selectivity in fMRI signal, but on a large scale rather than a finer, voxel based scale. However, although we found a very slight difference between activity arising from tangential and radial quadrants of our luminance stimuli, we found no difference at all for our chromatic stimuli. Thus it is very unlikely that our multivariate discrimination accuracy for chromatic gratings was based on such global signals. Note also that multivariate discrimination in the absence of any radial-tangential bias has been found previously using the protocol upon which this study was based (Haynes and Rees, 2005a, Fig. S3).

Instead, anisotropic distribution of orientation selective columns in visual cortex may lead to slight but reliable orientation biases in many fMRI voxels, which could be accumulated to enable above-chance classification of the activity patterns representing one orientation or another (Haynes and Rees, 2005a, 2006; Kamitani and Tong, 2005). Such slight biases would be sensitive to head movement, but this can be alleviated through the realignment and reslicing process during analysis so that some consistent information remains (see Fig. S6 in Haynes and Rees, 2005b). Interestingly, it has recently been reported that the voxels providing most information for orientation classification appear to correspond to draining veins on the cortical surface, suggesting that such veins may reflect orientation biases in the area of cortex they serve or may even show some specificity in the cortical columns they drain from (Gardner et al., 2006). However, in our study there appeared to be no systematic relationship between the orientation information carried by a voxel and its location within the retinotopic region activated by the stimulus (Fig. 5 and Fig. S3). These data are consistent with voxels sampling an anisotropic distribution of orientation columns.

Combined coding of chromaticity and orientation

Our principal finding was that distributed patterns of activity in human V1 could discriminate between chromatically defined orientations. Of course, human imaging techniques measure signals from relatively large neuronal populations, so our data show only that chromatically defined orientation information is represented in such signals from V1 and do not unequivocally determine whether individual cells show similar preferences. Nevertheless, our data are consistent with the hypothesis that colour-selective neurons also show some orientation specificity, in contrast to the traditional notion that features such as colour and orientation are represented separately in early visual cortex (e.g., DeYoe and Van Essen, 1985;

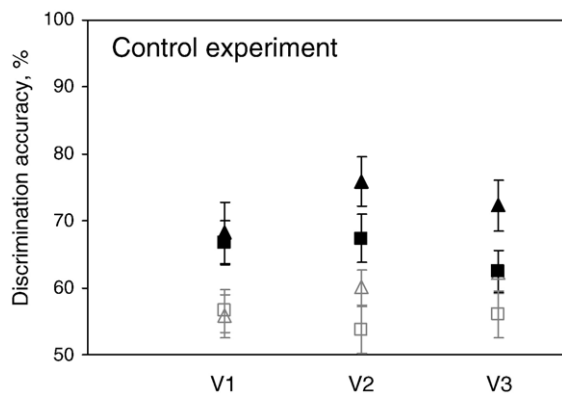


Fig. 6. Results for the control experiment. Solid symbols show discrimination accuracy for S-cone stimuli, while open symbols show discrimination accuracy for the luminance control stimuli (different shapes refer to each participant and error bars are s.e. within participant).

Landisman and Ts'o, 2002; Lennie et al., 1990; Livingstone and Hubel, 1988, 1984; Roe and Ts'o, 1999; Shipp and Zeki, 2002; Ts'o and Gilbert, 1988).

An alternate possibility is that orientation information is extracted from colour signals in later visual areas, and this orientation information is fed back to activate a population of V1 cells that do not represent the colour of the stimulus. However, such an explanation proposes that the very same V1 cells would reflect information about orientation independently from whatever chromaticity was used to define the stimulus — otherwise these cells would, by definition, have some combined chromatic and orientation selectivity. In such a situation, voxel activation biases useful for decoding orientation for L–M stimuli should also be useful for decoding orientation for S-cone stimuli (and vice versa). However, we found that discrimination was specific to the colour of the stimuli, and thus not consistent with the notion that the orientation-specific activity patterns we observed were conveyed by non-colour-selective neuronal populations.

In general the local spatial pattern of activity evoked by S-cone and L–M stimuli in V1 is expected to differ due to differences in the spatial distribution of the corresponding neuronal populations. However, this would not necessarily mean that the pattern of activity useful for decoding orientation would also differ between colours, if orientation information was in fact represented in the same neuronal population regardless of stimulus colour. Our finding of colour specificity in decoding orientation therefore implies that the orientation information being used in such discrimination comes from different neuronal populations. The most parsimonious explanation for this is that those neuronal populations are also colour-selective. It remains possible that differences in the spatial frequency sensitivity of each colour pathway might have caused a large discrepancy in the activity pattern useful for orientation discrimination, but the main power in our stimuli was within the range to which both colour systems are sensitive. Concerning the possibility of top–down feedback of orientation information, it is also interesting to note that a behavioural study has reported that colour-orientation contingent aftereffects can be obtained without the colours themselves being perceived (Vul and MacLeod, 2006), implying that the association of colour and orientation did not rely on high level binding and feedback.

Our results are therefore most consistent with an emerging view that the visual system is less segregated and modular than previously believed. In the case of orientation and the red–green (L–M) dimension of colour in particular, several studies indicate that macaque V1 seems to contain many cells with some selectivity for both features (Friedman et al., 2003; Gegenfurtner, 2003; Leventhal et al., 1995; Schluppeck and Engel, 2002). Furthermore, the fMRI signal in human V1 has been found to modulate with colour contrast adaptation that is specific for orientation (Engel, 2005).

Such an overlap in feature coding would be expected from an evolutionary point of view, in which the recently evolved distinction between M-cone information and L-cone information is carried to V1 not by its own dedicated “colour channel”, but through a preexisting channel, the parvocellular pathway, dedicated to supplying form information (e.g. Ghosh et al., 1996; Mollon, 1989; O’Keefe et al., 1998; Yamada et al., 1998, 1996). Since parvocellular inputs help build orientation specificity in V1, L–M information arrives in these orientation cells automatically. Thus it

makes sense that red–green colour information is never segregated from orientation information in V1, V2 or V3, and by implication, may not be segregated in any area of visual cortex.

Chromatic information from S-cone signals, on the other hand, arrives in V1 via koniocellular “colour channels” that are segregated from the pathways thought to provide the main inputs to orientation selective cells (Chatterjee and Callaway, 2003). There was therefore no anatomical or evolutionary reason to expect combined orientation and S-cone selectivity in V1, and there was little specific neurophysiological evidence reporting on this question (Friedman et al., 2003; Leventhal et al., 1995). Our findings suggest that combined coding of orientation and S-cone chromaticity may indeed exist in V1. Moreover, they indicate that orientation information in V1 is derived from the inputs of the S-cone pathways rather than orientation selectivity derived from luminance or L–M inputs simply being combined with non-oriented S-cone information on the basis of retinal location.

In addition to cells that may be sensitive to both chromaticity and orientation, V1, V2 and V3 are known to contain many colour neurons that show little or no orientation selectivity (e.g., Schluppeck and Engel, 2002). Our study is silent about these colour-only cells, and it is possible that they are the most important population for the perception of colour appearance, while colour-orientation cells contribute chiefly to the perception of orientation or edge detection (e.g., Conway et al., 2002). Thus, the *perception* of these features might still be based on independent processing, despite the existence of large numbers of cells that contain information about both. However, Engel (2005) found agreement between fMRI signal changes and measurements of colour appearance following adaptation to oriented chromatic stimuli. Both measures showed a component of chromatic adaptation that was not orientation selective and a component that was, suggesting that both oriented and unoriented colour neurons contribute to colour perception.

It is also worth noting that although the two chromatic dimensions we have studied (L–M and S-cone) are based on the physiological signals entering V1, these dimensions do not have any special significance in colour appearance (it is a common misconception that they correspond to opponent processing of perceptually “unique hues” red, green, blue and yellow, but they do not, as Fig. 1 illustrates). Indeed, many cells even in V1 show evidence of combining L–M and S-cone input. Similarly, some V1 cells are responsive to both luminance and chromaticity. Thus the discrimination performance we have measured for luminance and the two chromatic axes may not be based on neuronal populations that uniquely favour these input dimensions. Similarly, we cannot know from our data whether cells with sensitivity to both colour and orientation may not also be sensitive to other features such as motion or depth.

Ruling out luminance artefact

It is difficult to restrict information to chromatic pathways because the magnocellular pathway, for example, is very sensitive to edges, even equiluminant ones (Logothetis et al., 1989). For this reason we embedded our oriented chromatic gratings in luminance noise so that for luminance pathways all the edges of all the squares within our stimuli were visible and always changing, and thus only chromatic pathways would pick out the chromatic edges oriented in one or other direction (Birch et al., 1992; Mollon,

1982). A further difficulty is presented in the fMRI environment by poor spatial uniformity in LCD projectors. Our control experiment measured the upper limit of discrimination performance that might have been produced by any resultant luminance artefact in the S-cone stimuli, if it had extended across the whole stimulus rather than being confined to parts of the stimulus. We found that some degree of discrimination was possible even for the low contrast control stimulus, but it was not sufficient to explain the discrimination level of the chromatic orientations. Furthermore, if discrimination of S-cone stimuli was based on luminance artefact, we might expect similarly successful discrimination for training on luminance stimuli and testing with S-cone stimuli. However, this was not the case.

Comparison across ROIs and stimuli

Discrimination accuracy for chromatically defined orientation was comparable for V1, V2 and V3. However, this does not necessarily mean that similar numbers of neurons have combined colour and orientation selectivity in each area. Direct comparisons between the areas are complicated by differences in size and functional architecture, and it is possible that discrimination was based on different causes in each area. Even if the basis of discrimination is the same in each area, such as voxel biases produced by anisotropy in the underlying neuronal orientation columns (Haynes and Rees, 2005a; Kamitani and Tong, 2005), discrimination performance would be affected by the spatial distribution of such columns across the region of interest and how sharply they are defined. Thus approximately equal performance across areas may have arisen from a combination of factors, some of which might act to reduce discrimination ability from V1 to V3 (such as, for example, less clearly defined columns) and some of which might act to increase discrimination performance (such as, for example, more integration of orientation and colour information).

Discrimination accuracy was also similar for each chromatic axis, while accuracy for the luminance stimuli was slightly greater. However, direct comparisons are complicated by the fact that there is no sure way of equating these different stimulus dimensions. Equal multiples of cone contrast threshold, for example, do not necessarily map well onto suprathreshold salience. It is interesting, though, that the S-cone stimuli produced good discrimination despite the relatively small number of koniocellular projections carrying S-cone information to V1. This is consistent with data from macaque V1 that suggest that there is considerable amplification of the S-cone contribution at the V1 stage (De Valois et al., 2000).

Conclusion

The data reported here are most parsimoniously explained by combined orientation and chromatic information in human V1, not only for the L–M (red–green) chromatic axis, but also for S-cone signals. This is especially interesting given that S-cone signals are not thought to contribute greatly to form perception, and their projection to V1 is relatively weak and clearly segregated from the pathways known to supply form information. These results do not support the established doctrine of segregated form and colour processing in early visual cortex and support instead the idea that many cells at all levels show joint selectivity for different visual features.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2007.09.013](https://doi.org/10.1016/j.neuroimage.2007.09.013).

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