



UNIVERSITÀ  
DEGLI STUDI  
FIRENZE

# FLORE

## Repository istituzionale dell'Università degli Studi di Firenze

### **BOLD human responses to chromatic spatial features**

Questa è la Versione finale referata (Post print/Accepted manuscript) della seguente pubblicazione:

*Original Citation:*

BOLD human responses to chromatic spatial features / Castaldi E.; Frijia F.; Montanaro D.; Tosetti M.; Morrone M.C.. - In: EUROPEAN JOURNAL OF NEUROSCIENCE. - ISSN 0953-816X. - ELETTRONICO. - 38:(2013), pp. 2290-2299. [10.1111/ejn.12223]

*Availability:*

The webpage <https://hdl.handle.net/2158/1242093> of the repository was last updated on 2021-09-04T05:10:56Z

*Published version:*

DOI: 10.1111/ejn.12223

*Terms of use:*

Open Access

La pubblicazione è resa disponibile sotto le norme e i termini della licenza di deposito, secondo quanto stabilito dalla Policy per l'accesso aperto dell'Università degli Studi di Firenze (<https://www.sba.unifi.it/upload/policy-oa-2016-1.pdf>)

*Publisher copyright claim:*

La data sopra indicata si riferisce all'ultimo aggiornamento della scheda del Repository FloRe - The above-mentioned date refers to the last update of the record in the Institutional Repository FloRe

(Article begins on next page)

## NEUROSYSTEMS

# BOLD human responses to chromatic spatial features

E. Castaldi,<sup>1</sup> F. Frijia,<sup>2</sup> D. Montanaro,<sup>2</sup> M. Tosetti<sup>3</sup> and M. C. Morrone<sup>4,5</sup><sup>1</sup>Department of Neuroscience, Psychology, Pharmacology and Child health, University of Florence, Firenze, Italy<sup>2</sup>Fondazione CNR/Regione Toscana G. Monasterio, Pisa, Italy<sup>3</sup>Stella Maris Scientific Institute, Pisa, Italy<sup>4</sup>Department of Translational Research on New Technologies in Medicine and Surgery, University of Pisa, Pisa, Italy<sup>5</sup>Robotics, Brain and Cognitive Sciences Department, Fondazione Istituto Italiano di Tecnologia, Genova, Italy**Keywords:** colour, functional magnetic resonance imaging, human visual cortex, scene perception, spatial phase

## Abstract

Animal physiological and human psychophysical studies suggest that an early step in visual processing involves the detection and identification of features such as lines and edges, by neural mechanisms with even- and odd-symmetric receptive fields. Functional imaging studies also demonstrate mechanisms with even- and odd-receptive fields in early visual areas, in response to luminance-modulated stimuli. In this study we measured fMRI BOLD responses to 2-D stimuli composed of only even or only odd symmetric features, and to an amplitude-matched random noise control, modulated in red–green equiluminant colour contrast. All these stimuli had identical power but different phase spectra, either highly congruent (even or odd symmetry stimuli) or random (noise). At equiluminance, V1 BOLD activity showed no preference between congruent- and random-phase stimuli, as well as no preference between even and odd symmetric stimuli. Areas higher in the visual hierarchy, both along the dorsal pathway (caudal part of the intraparietal sulcus, dorsal LO and V3A) and the ventral pathway (V4), responded preferentially to odd symmetry over even symmetry stimuli, and to congruent over random phase stimuli. Interestingly, V1 showed an equal increase in BOLD activity at each alternation between stimuli of different symmetry, suggesting the existence of specialised mechanisms for the detection of edges and lines such as even- and odd-chromatic receptive fields. Overall the results indicate a high selectivity of colour-selective neurons to spatial phase along both the dorsal and the ventral pathways in humans.

## Introduction

One of the major tasks of the human visual system is to identify the most salient information in an image, such as edges and lines, and use it to segment the image into surfaces and shapes as a first stage towards scene analysis.

Local contrast is an important property for tagging salient parts of the scene but it is not the only important one. Two images with the same power spectra, and hence the same contrast, are equally detectable but can carry completely different information. A classical demonstration is provided by experiments showing that the recognition of an image is not determined by their amplitude spectra but rather by their phase spectra (Wichmann *et al.*, 2006; Oppenheim & Lim, 1981; Piotrowski & Campbell, 1982; Morgan *et al.*, 1991).

Measurement of the blood oxygen level-dependent (BOLD) signal modulation to natural images and to degraded versions of them obtained by scrambling the phase spectrum by various amounts demonstrated a stronger activity for the natural images than the full phase-scrambled noise pattern in primary visual cortex (V1) and extrastriate visual cortex (V2, V3, V3A and V4) and in the anterior

bank of the superior temporal sulcus (STS) both in monkey (Rainer *et al.*, 2001, 2002) and in human (Olman *et al.*, 2004; Perna *et al.*, 2005, 2008; Tjan *et al.*, 2006; Henriksson *et al.*, 2009).

The preference for natural images is a consequence of the local phase-selectivity of the individual neuron, achieved by the symmetry and bandwidth of the neuronal receptive field (Hubel & Wiesel, 1962; Movshon *et al.*, 1978a,b; Field & Tolhurst, 1986; Gaska *et al.*, 1987; Jones *et al.*, 1987; Pollen *et al.*, 1988; Mechler *et al.*, 2002, 2007; Ringach, 2002, 2004; Felsen *et al.*, 2005). In natural images, and for each local feature, the local phase congruency between harmonics is higher than in random patterns (Burr *et al.*, 1989, 1992; Morrone *et al.*, 1993; Martini *et al.*, 1996; Perna & Morrone, 2007). Higher phase-congruency generates a stronger neuronal response, as has been quantitatively modelled by the local energy model (Morrone & Burr, 1988).

While the electrophysiological and psychophysical literature on phase selectivity is quite extensive in both humans and animals, very few functional magnetic resonance imaging (fMRI) investigations have been performed. In particular there is only one study that has investigated the selectivity of the BOLD response for stimuli that locally differ only in the average phase value. Perna *et al.* (2008) manipulated the local phase of checkerboard stimuli to generate patterns with equal power spectra, equal salience and equal spatial structure but which were totally different in appearance.

Correspondence: Dr M. C. Morrone, as above.

E-mail: concetta@in.cnr.it

Received 12 December 2012, revised 11 March 2013, accepted 20 March 2013

Comparing the BOLD response to the original checkerboard stimulus vs. the transformed pattern, which appeared as a grid of thin lines and four-pointed stars, they showed that only two associative cortices, the dorsal lateral occipital complex (dLO) and the caudal part of the intraparietal sulcus (CIP) code the average phase of the stimuli. Interestingly, the two patterns gave equal responses in V1. The absence of modulation of activity to the stimulus alternation (Perna *et al.*, 2005) suggests that an equal number of neurons with even- and odd-symmetry receptive fields (RFs) are activated by the two stimuli.

In agreement with monkey and cat results (Mechler *et al.*, 2002, 2007; Ringach, 2002; Felsen *et al.*, 2005), this imaging study indicates that the phase congruency for luminance-modulated stimuli in humans is encoded early, at the level of the primary visual area, while only higher-order visual areas, such as dLO and CIP, are required to discriminate between stimuli with different phase and local symmetry, such as edges from lines. The preference for edges may reflect the higher frequency of occurrence of these features in natural images (Bell & Sejnowski, 1997).

Similar arguments can be applied to patterns that are modulated only in chromaticity and not in luminance. Most theories of early visual analysis assume shape and colour are analysed by specialised detectors located in dedicated parallel pathways. Neuroimaging studies in humans have demonstrated that colour-opponent mechanisms are already present in V1 and V2 (Kleinschmidt *et al.*, 1996; Engel *et al.*, 1997; Engel & Furmanski, 2001; Schluppeck & Engel, 2002) and that they are selective for orientation (Sumner *et al.*, 2008; McDonald *et al.*, 2010). The chromatic responses are more prominent along the ventral pathway (also after equating for detectability or cone-contrast) than the dorsal pathway, where nevertheless a genuine response to colour is present (Liu & Wandell, 2005; Mullen *et al.*, 2007, 2010; D'Souza *et al.*, 2011). Psychophysical experiments have demonstrated that phase discrimination is as good for chromatically as for luminance-modulated patterns, once the contrast is equated for stimuli detectability (Martini *et al.*, 1996). Similarly, adding phase-noise to the spectra of natural images has a stronger disruptive effect on the classification of natural coloured images than simply reducing the image contrast (Wichmann *et al.*, 2006). Good phase discrimination of chromatic stimuli has also been demonstrated measuring human visual evoked potentials (VEPs) to jittered counter-phased red–green equiluminant gratings (Girard & Morrone, 1995). In the present study we aim to determine the level in the colour pathways at which the selective responses to phases emerge, and whether the colour system shows a BOLD preference for phase-congruent stimuli, as does the luminance system.

The results suggest equal sensitivity to random- and congruent-phase of equiluminant patterns in V1, and a preference for equiluminant odd-symmetry features (absolute phase around  $\pm 90^\circ$ ) along both the ventral and dorsal pathways, implicating these pathways even in the analysis of equiluminant feature and surfaces.

## Materials and methods

### Visual stimuli

Three different kinds of stimuli were used in the experiment. There were two experimental congruent-phase stimuli (which we label even-symmetry and odd-symmetry stimuli) and a control random-phase stimulus (noise stimulus), as shown in Fig. 1.

The congruent-phase stimuli were obtained by multiplying two orthogonal vertical and horizontal gratings synthesised from 19 odd sine harmonics (first, third, fifth ...  $n$ th) of  $1/n$  amplitude. For the local

odd-symmetry stimuli the 19 harmonics all had the same absolute phase, equal to  $\pi/2$  (square wave), while for the local even symmetry stimuli it was equal to zero. To minimise chromatic aberrations, the high spatial frequencies were attenuated with a Gaussian filter in both the colour- and the luminance-modulated stimuli.

$$F(\omega_x, \omega_y) = e^{-\frac{(\omega_x^2 + \omega_y^2)}{2\sigma^2}}$$

where  $\sigma = 5.5$  cycles/° was applied to both the  $\omega_x$  and the  $\omega_y$  frequency axes.

For all 2-D stimuli, the amplitude of the fundamental harmonics (spatial frequency: 0.37 cycles/° and  $45^\circ$  orientation) were halved to reduce the relative contributions of the first harmonics to the response. To reliably measure phase selectivity it is important that each visual channel responds simultaneously to many harmonic components, and this would not be the case for stimuli comprising predominantly first harmonics (for details see Burr *et al.*, 1989).

The 2-D odd-symmetry stimulus comprises only edges, and looked like a checkerboard (Fig. 1A and D) while the 2-D even-symmetry stimulus looked like a grid of thin lines that form stars (Fig. 1B and E). The even and the odd stimuli at each point had the same local root-mean-square (RMS) contrast and by construction had the same local phase congruency between harmonics and also the same number of salient features, being 1-D edges, 1-D line, 2-D stars or 2-D edge junctions. The local phase congruency can be estimated by computing the local energy (Morrone & Burr, 1988) which for these patterns is given by the square root of the sum of the square of the even- and odd-symmetry functions (see Morrone & Burr, 1997). Figure 1 shows the result of the local energy function for a particular row of the 2-D stimuli: the energy (and hence the local RMS) peaks along the major horizontal and vertical salient features. To a first approximation, the linear response of a V1 population of simple cells with even-symmetric and odd-symmetric RFs will be maximum for the even-symmetry stimuli and odd-symmetry stimuli respectively. The response of complex cells, with ON-OFF subunits, will approximate more closely the local energy function (Hubel & Wiesel, 1962; Movshon *et al.*, 1978a,b; Pollen & Ronner, 1981; Spitzer & Hochstein, 1985).

For the random-phase stimulus, the phase of each harmonic of the 2-D congruent-phase stimuli was shifted by a random value. This procedure generated 2-D stimuli with equal global power spectra and equal global RMS contrast. Examples of the random 2-D noise stimuli of matched power spectra are shown in Fig. 1C and F. These stimuli did not have strong salient features and the local energy function was more distributed in space with small amplitude peaks.

RMS contrast, defined as SD of luminance divided by the mean, was equal for all these stimuli to within 5.16%. However, luminance Michelson contrast (defined as the difference between the maximum and minimum luminance divided by their sum) was very different, being 17% for edge stimuli and 86% for line stimuli. The noise stimuli had on average intermediate Michelson contrasts of 30%.

The stimuli were modulated in luminance by driving the red and the green monitor channels in phase and setting to zero the blue channel. The equiluminant (red–green) checkerboards were obtained by modulating red and green monitor channels in anti-phase. The Commission Internationale de l'Eclairage coordinate for the red and green guns were  $x = 0.665$ ,  $y = 0.312$  and  $x = 0.244$ ,  $y = 0.55$  respectively. The CIE coordinates for the average yellow background were  $x = 0.374$ ,  $y = 0.479$ . The mean luminance was 42 cd/m<sup>2</sup>. Equiluminance subjective point was assessed for each scanning

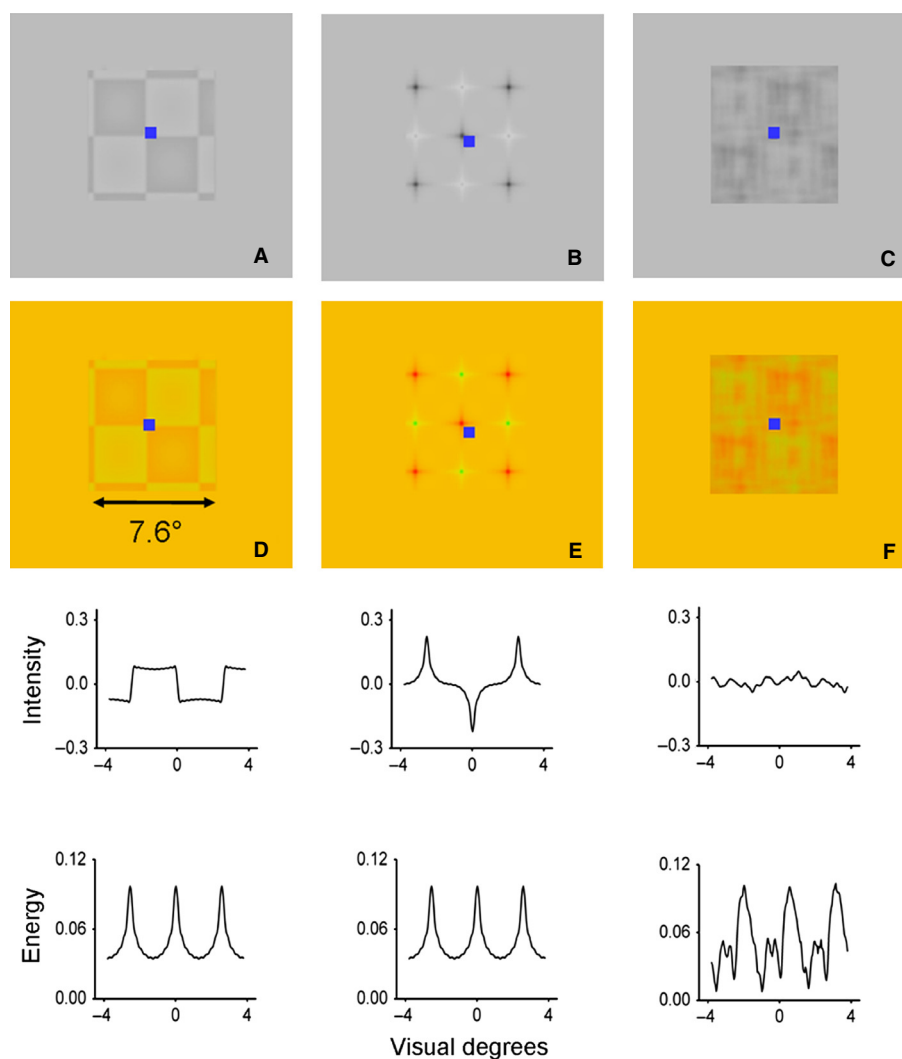


FIG. 1. Visual stimuli. Examples of the visual stimuli. Red and green gun modulation were summed in phase to create luminance checkerboards (top row) and in anti-phase to create the equiluminant checkerboards (bottom row). (A and D) Example of the odd-symmetry stimulus: two-dimensional filtered checkerboard, comprising  $2 \times 2$  periods each subtending  $3.8 \times 3.8^\circ$  of visual angle. (B and E) Example of the even-symmetry stimulus where each individual edge (odd-symmetry feature) of A and D was transformed in a feature with local even symmetry. (C and F) Noise stimuli obtained by randomising the phase of each harmonic. All stimuli had the same RMS contrast but different Michelson contrast. The even- and odd-symmetry image pairs always had the same RMS local contrast for each individual spatial position, despite the illusory different appearance. The integral of the power over space was equal for the three stimuli, while the Michelson contrasts were equal to 17%, 86% and 30% for the odd and even symmetry and the random stimulus respectively. The lower traces show examples of the luminance modulation and the output of the local energy function for the same row of the images.

session and each subject inside the scanner by flicker photometry. At equiluminance the cone contrast (RMS of L and M cone contrast) was a factor of 1.8 lower than the luminance contrast.

$2 \times 2$  periods (each subtending  $3.8 \times 3.8^\circ$  of visual angle) of the 2-D stimuli were displayed. Because the equiluminance point changes with eccentricity, we restricted the stimulus to a central window of  $7.6^\circ \times 7.6^\circ$  ( $237 \times 237$  pixels, windowing with no edge-smoothing to display complete stimulus periods) while the remaining area (covering the  $800 \times 600$  pixel resolution monitor) was kept at constant chromaticity and luminance. Inside this window, the coherent-phase stimuli were jittered to a random position every 2.5 s to avoid BOLD adaptation; for the non-coherent phase stimuli a new draw of random phase was selected every 2.5 s and the new stimulus synthesised and displayed.

Stimuli were designed using Matlab 7.5.0 R2007b with Psychtoolbox (Brainard, 1997) installed on an Asus F3JA notebook

computer with an integrated 32-bit precision graphics card (ATI Radeon X1600) and 60-Hz temporal refresh rate.

The computer was connected with a Polaroid Polaview 220 DLP projector with a lens that projected from 7.5 m to a screen inside the scanner bore 45 cm from the observer's eyes. The projected image was gamma-corrected to ensure linearity. We verified linearity by direct luminance measurements at the screen.

In an additional experiment in which we measured the response for various red/green ratios (CIE coordinates for the red and green stimuli were  $x = 0.577$ ,  $y = 0.357$  and  $x = 0.292$ ,  $y = 0.537$  respectively and mean luminance  $48 \text{ cd/m}^2$ ), we displayed the stimuli through NordicNeuroLab's VisualSystem goggles ( $800 \times 600$  pixels, with a refresh rate of 85 Hz) after adequate gamma correction. The colour-luminance contrast ratio of the pattern was varied by changing the modulation of the green, keeping constant the modulation of the red.

The mean luminance of both red and green guns remained unchanged with colour ratio. A ratio of 0.5 indicates that the luminance modulation of the green gun was half that of the red gun.

### Retinotopic maps

Retinotopic mapping and localiser scans were performed on each subject in a separate experimental session.

To identify the representation of vertical and horizontal meridians one hundred circular dots (0.3° diameter), half black and half white, on a grey background, moved within two symmetrical sectors across the fixation point along the two principal meridians (for details see d'Avossa *et al.*, 2007; Crespi *et al.*, 2011). Each dot had a 20-frame lifetime at refresh rate of 60 Hz (333 ms). Locally, the dots moved along linear trajectories at a constant speed of 10°/s; globally they were perceived to follow an expanding or contracting movement along the vertical and horizontal meridians spanning 20° of visual angle. When each dot's lifetime expired, or its trajectory ended outside the sector, the dot was regenerated in another position randomly chosen in order to maintain a uniform density of 0.44 dots per square degree of visual angle.

To activate selectively the representation of the upper, lower, right and left visual hemifields, 250 dots were displayed with radial motion (same dimensions and lifetime as for the meridian stimulus) within each circular sector of  $\pm 40^\circ$ , symmetric around the diagonal of the quadrant.

Each meridian or hemifield stimulation lasted 15 s, with motion direction inverted seven times to avoid BOLD adaptation. Each block was repeated six times.

Identification of the different retinotopic maps was conducted on the basis of the upper–lower visual field representation and on the vertical–horizontal reversal, in accordance with standard retinotopy literature (Serenio *et al.*, 1995; Engel *et al.*, 1997; Hadjikhani *et al.*, 1998; Press *et al.*, 2001; Tootell & Hadjikhani, 2001; Wade *et al.*, 2002; Wandell *et al.*, 2005; Hansen *et al.*, 2007). To localise V4 we used the criterion proposed by Hansen *et al.* (2007), which considers the representation of part of the lower visual field in the dorsal cortex abutting V3d, in addition to standard retinotopic localisation.

The CIP and transversal occipital sulcus (TOS) were defined as anatomically located along the specific sulci and by including all the voxels that were active for the alternation of blank against even-symmetry and odd-symmetry stimuli, modulated either in luminance or in colour. Usually the selected area was about  $4 \times$  larger than the localiser, if this did not interfere with an adjoining region of interest (RoI).

The human Middle Temporal Complex and dLO were localised using 100 moving dots (speed 10°/s, 0.5° diameter). These dots moved randomly for 21 s and then followed a coherent spiral movement (flow motion) changing from expansion to clockwise, contraction and anti-clockwise circular motion twelve times in 21 s. These dots covered a circular patch of 15° diameter. Each dot had a limited lifetime of 10 frames (166 ms), after which it disappeared to be reborn in a new random position. Each acquisition sequence comprised six presentation for the coherent and six for the incoherent motion.

To localise the region of interest representing the stimulus patch within the retinotopic visual areas, a blank stimulus of the same chromaticity was compared against the two experimental congruent-phase stimuli. The border of the activity ( $P < 0.001$ ) elicited by this localiser was then traced in V1.

### Subjects and procedure

Seven healthy adults (six females, one male) with normal colour vision and normal or corrected-to-normal acuity were the subjects

of the experiment. For each subject the equiluminant point was measured independently inside the scanner using flicker photometry, displaying a red–green sine wave grating flickering at 7.55 Hz and varying the modulation of the green gun keeping the red gun modulation fixed (the subjective equiluminant point defined by the ratio of the two gun modulations was always between 0.52 and 0.54).

Informed written consent was obtained for each subject prior to scanning sessions, in accordance with the guidelines of the MRI Laboratory, Fondazione CNR/Regione Toscana G. Monasterio, Pisa. The studies were approved by the ethics committee of the Azienda Ospedaliero-Universitaria Pisana (protocol number 3255, approved on 20/01/2009) and was in accordance with the ethical standards of the 1964 Declaration of Helsinki.

fMRI measurements were performed on a 3-T scanner (GE Excite HDx) equipped with an eight-channel brain coil. Each session began by acquiring a set of anatomical images of whole brain with T<sub>1</sub>-weighted contrast. A fast spin-echo sequence was used with TR, 10.8 ms; TE, 4.9 ms; flip angle, 13°; FOV,  $256 \times 256$  mm<sup>2</sup>; slice thickness, 1 mm; bandwidth, 15.63 Hz; and an isovoxel matrix size of  $256 \times 256$ . The data acquisition time was 5.56 min.

Echo planar imaging (EPI) sequences were used for the fMRI data acquisition (TR, 2.5 ms; TE, 40 ms; FOV,  $240 \times 240$  mm; flip angle, 90°; matrix size,  $128 \times 128$ ; and slice thickness, 4 mm; 96 volumes).

In a block design we presented four different stimuli sequences in random order. In two sequences, one modulated in luminance and the other in colour contrast, the random-phase stimuli (OFF-block) were compared against two congruent-phase stimuli (ON-block, with the even- and odd-symmetry stimuli selected randomly at equal probabilities). In the other two sequences, one modulated in luminance and the other in colour contrast, the two congruent-phase stimuli were compared with each other: even-symmetry stimulus (OFF-block) against odd-symmetry stimulus (ON-block). Each subject performed from two to four scans per condition. We also ran a localiser in which a blank equiluminant field of the same chromaticity (OFF-block) was compared with the two experimental congruent-phase stimuli (ON-block). The OFF- and ON-blocks alternated six times and each block lasted 20 s. Within each block the stimuli jumped from one random spatial position to another every 2.5 s in order to avoid BOLD-signal adaptation. For all conditions, we asked subjects to fixate on a stable target that remained in the centre of the visible screen for the entire scan duration. Head movements were minimised by padding and tape.

A non-commercial software package, 4DFF, from Neuro-Imaging Laboratory (Washington University, St Louis, MO, USA) was used for the pre-processing of the imaging data. To compensate for systematic slice-dependent differences in acquisition time, functional data were temporally interpolated and re-sampled; slice intensity differences caused by interleaved acquisition were eliminated. Overall image intensity was normalised within scans to a standard value of 1000 to compensate for inter-scan intensity differences. Functional images were corrected for three-dimensional motion by realigning data within and across scans and sessions with reference to the first realigned volume of the first scan, using a six-degrees-of-freedom rigid body transformation.

BOLD images were spatially normalised according to the atlas of Talairach & Tournoux (1988) to obtain standardised coordinates for the RoI. Lastly, data were spatially re-sampled to a cubic voxel with a resolution of 2.0 mm<sup>2</sup>.

Brain Voyager qx (version 2.2 Copyright © 2001–2011; Rainer Goebel, Brain Innovation B.V., Maastricht, The Netherlands) was



used to generate flat representations of the cortical surface and for statistical analysis. To generate flat maps for each hemisphere the white–grey boundary was traced, using an automatic segmentation algorithm supplemented by manual correction by an expert operator to correct errors generated by the automatic routine. This segmentation was also used to automatically reconstruct the surface of the outer grey-matter boundary, which was subsequently inflated and flattened by geometric projection.

For all scans an initial qualitative analysis was performed applying a general linear model to a boxcar model convolved with a canonical hemodynamic response function (HRF). We marked significant variations in response with a threshold set to  $P < 0.02$  and cluster size to  $3 \times 3$  voxels. This permissive threshold was selected to mark even noisy response variation in V1. This analysis was used to determine the Talairach coordinates of the foci activities reported in Table 1. For primary visual areas the average response was modulated to the second harmonic, which could not be revealed by general linear model analysis without changing the boxcar model. For quantitative analysis the response was evaluated by averaging the BOLD signal in anatomical areas defined on independent criteria. For each ROI we averaged the BOLD time-courses across subjects for the entire sequence of stimuli alternations and runs. The first and second harmonic amplitudes of each average profile were then computed by projecting them along the first and second harmonic phase of a modelled response, calculated by convolving the boxcar stimulus sequence with the canonical HRF. A sign test was performed on the projected harmonic amplitude by bootstrapping (Efron & Tibshirani, 1993), resampling the individual runs (with replacement) and repeating the process 2000 times, for all the areas and all stimulus conditions.

Results

It is always difficult to compare directly the activity elicited by colour- and luminance-modulated stimuli because the contrast and the visual salience of the two sets of stimuli are different, even when equated for detectability. The best strategy is to study independently how the phase manipulation affects the BOLD response. We used stimuli that were equated for visibility so as to equate average activity to the colour- and luminance-contrast modulated stimuli.

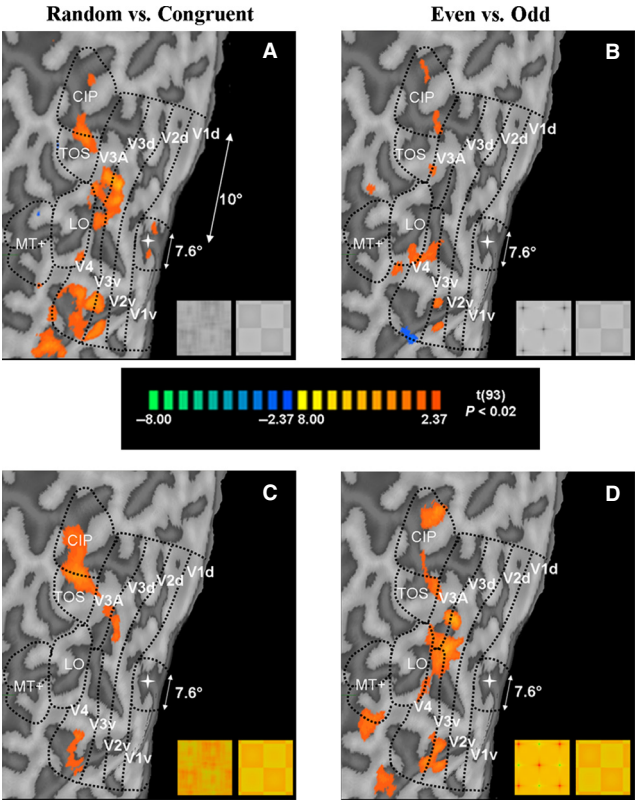


FIG. 2. Activations on flat map for subject S1. Typical patterns of activation elicited by contrasting random-phase stimuli against congruent-phase stimuli (left) and contrasting even-symmetry against odd-symmetry stimuli (right) both for luminance (upper) and for colour (lower) conditions, displayed on the flat map of subject S1, with  $P < 0.02$ . Contrasting random against congruent-phase stimuli elicited activation changes in the primary visual cortex only for the luminance condition. The modulation was not present in any of the other stimulus conditions. Both dorsal and ventral pathway activities were strongly modulated by the equiluminant stimuli as well as by luminance-contrast stimuli.

Figure 2 illustrates qualitatively the overall effect of phase manipulation on the visual stimuli in one subject. Figure 2A and B reports the data for luminance-modulated stimuli and Fig. 2C and D for

TABLE 1. Highest foci of activity (Talairach coordinates)

		V3A			CIP			TOS			LO			V4		
		x	y	z	x	y	z	x	y	z	x	y	z	x	Y	z
S1	Left	−28	−89	12	−31	−68	24	−33	−76	15	−36	−79	−6	−25	−85	−11
	Right	31	−86	12	30	−65	23	34	−81	11	31	−85	−4	27	−82	−8
S2	Left	−22	−89	19	−21	−70	23	−30	−75	18	−33	−77	3	−34	−84	−4
	Right	26	−75	17	22	−75	29	33	−80	9	40	−72	−3	36	−80	−2
S3	Left	−33	−83	11	−29	−72	33	−42	−73	10	−41	−76	−3	−34	−83	−6
	Right	30	−81	16	25	−64	29	37	−70	9	42	−73	−8	32	−80	−4
S4	Left	−29	−79	15	−25	−71	36	−31	−66	15	−34	−78	−9	−32	−81	−6
	Right	20	−74	13	25	−67	32	33	−69	19	39	−73	−6	33	−86	−9
S5	Left	−23	−87	13	−24	−78	20	−31	−87	12	−26	−89	6	−32	−79	−6
	Right	25	−88	16	22	−76	30	32	−76	15	35	−83	−4	30	−86	−3
S6	Left	23	−81	17	−29	−68	24	−37	−82	19	−40	−80	−9	−35	−81	1
	Right	28	−82	12	27	−67	29	39	−75	9	39	−72	1	30	−82	−4
S7	Left	−26	−80	11	−27	−68	32	−40	−82	7	−39	−87	−3	−25	−87	−9
	Right	22	−86	15	30	−65	22	37	−83	8	39	−87	−3	20	−80	−7

equiluminant stimuli. The individual cortical areas are segmented on retinotopic criteria and are relatively large with respect to the activation elicited from our small stimuli.

When modulated in luminance (Fig. 2A), the alternation between random-phase and congruent-phase stimuli elicited a change in activation in primary visual cortex. The response was located inside the region representing the central 7° of visual field, revealed by alternating congruent-phase stimuli against blank fields of matched mean chromaticity and luminance. The dashed lines in V1 mark the peak border activities of this localiser with  $P < 0.001$ , while the response modulation to the luminance congruent-phase stimuli covers the foveal representation (indicated by a star in Fig. 2A). This result is consistent with the central activity measured by Perna *et al.* (2008) despite the more extended area of their stimuli (15°). However, the primary visual cortex modulation of activity was no longer present when the same stimuli were modulated in colour contrast (Fig. 2C), despite the low threshold used ( $P < 0.02$ ).

The alternation of random- against coherent-phase stimuli, modulated both in chromaticity and in luminance, activated many associative areas along both the dorsal and the ventral pathways. We observed changes in activation along the dorsal stream, mainly in V3A, CIP, TOS and dLO. Along the ventral stream the activation changes were mainly located in V4. All these areas showed a stronger response for coherent stimuli than for random stimuli (Fig. 2A and C).

No change in response was observed in V1 when the stimuli were modulated in average phase, alternating between even- and odd-symmetry stimuli. A preference for the stimulus comprising odd-symmetry visual features ( $\pm 90^\circ$  average phase) was observed at higher cortical levels. Indeed, both the ventral and the dorsal pathways (V3A, CIP, TOS, dLO and V4) were more strongly activated by this stimulus both for equiluminant and luminance contrast modulation.

Table 1 shows the Talairach coordinates of the hot-spots of activation inside the RoI of these areas. The consistency between subjects is also strong for areas that could not be retinotopically segmented, such as TOS and CIP.

The average modulation of BOLD signals over the seven subjects, measured within the V1 RoI responding to the stimulus patch, is shown in Fig. 3 (top row). The response to random- vs. congruent-phase stimuli modulated in luminance showed a dominant first-harmonic modulation of the BOLD signal, with a preference for congruent stimuli. The amplitude of modulation, projected on the direction of the presumed hemodynamic response of the boxcar model (Fig. 4, top left), was significantly ( $P < 0.05$ ) different from zero.

The V1 first harmonic response of the same voxel group (V1F; representing 7° of eccentricity) was not evident for either colour condition, nor for even- vs. odd-symmetry stimuli modulated in luminance (Fig. 3, top row). Neither this central region of V1, nor the entire V1, showed a significant response modulated on the first harmonic. The time course showed a modulation, but it was in synchrony with the second harmonic, without a clear preference for congruent stimuli or for edges: the activity was stronger after each transition of stimuli, producing two peaks for each full period of alternation. The response on the second harmonic ( $P < 0.05$  for average phase alternation) was statistically significant and present for both the colour- and luminance-modulated stimuli (Fig. 4). This suggests that the repetition of the same stimulus in each block caused adaptation which recovered when the stimulus changed, indicating a selectivity for the phase of the stimuli in the central representation of the visual field. The pattern of the average results was different for V4 (Fig. 3, bottom row). The responses showed strong and significant BOLD modulations in all conditions (Fig. 4), both for luminance- and chromatic-modulated stimuli, with a preference for congruent-phase stimuli in the conditions over random-phase

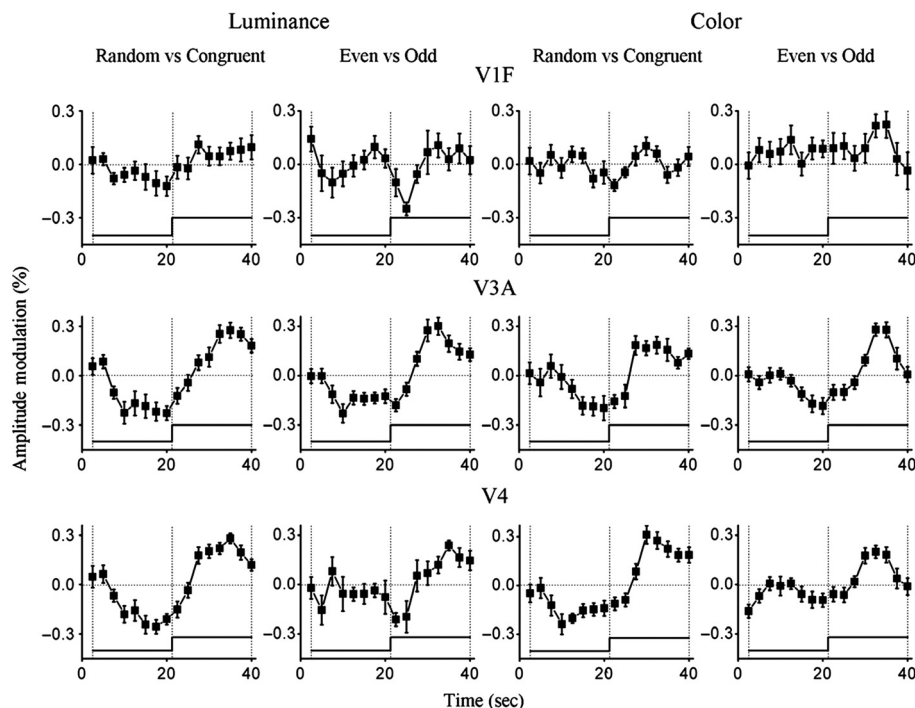


FIG. 3. Averaged V1F, V3A and V4 BOLD time-courses. BOLD time-courses, averaged across all subjects' hemispheres and runs for the 7° central V1 (first row), V3A (second row) and V4 (third row) RoIs (defined by retinotopy), for the various conditions. For each subject the number of runs varied between two and four for each condition. The error bars represent 1 SEM. The transition of the stimulus is represented by the step waveform and marked by dashed lines.

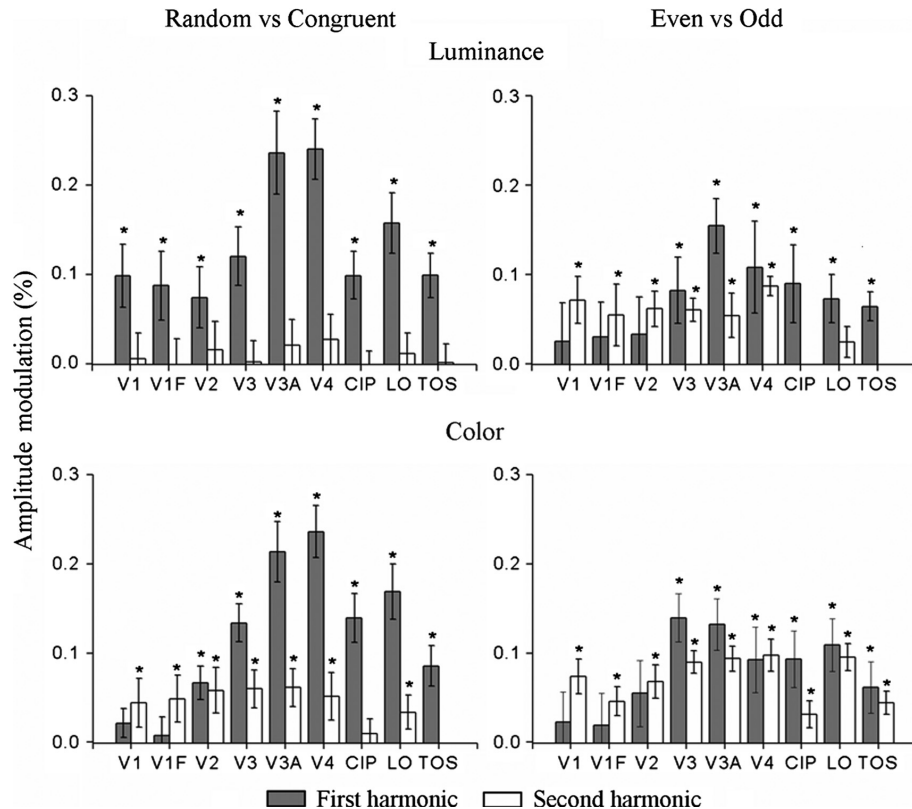


FIG. 4. First and second harmonic amplitude. Bar plot of the first (gray) and second (white) harmonic amplitude projected along the phases of the corresponding hemodynamic components for all areas and conditions. The mean of the projected amplitudes was calculated across subjects' hemispheres and runs; the error bars report the error of the mean evaluated by bootstrap. A significant ( $*P < 0.05$ ) first-harmonic amplitude modulation was observed in V3A, CIP, TOS, LO and V4 for all conditions. In the central  $7^\circ$  representation of V1 the first-harmonic modulation was significant ( $*P < 0.05$ ) only for the random-phase vs. congruent-phase luminance condition, while the second-harmonic modulation was prevalent in all the other conditions.

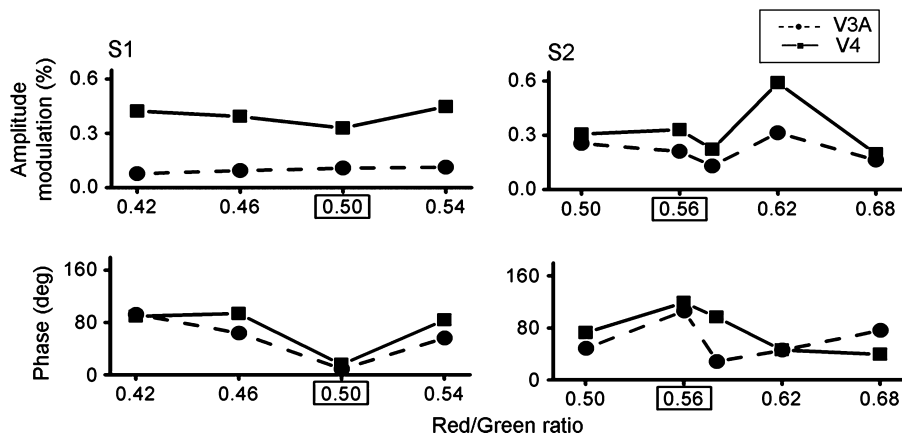


FIG. 5. BOLD response amplitude as a function of the red : green colour ratio. V3A and V4 BOLD response amplitude and phase to random- vs. congruent-phase stimuli modulated in colour stimuli as a function of the red : green colour ratio for two subjects.

stimuli and also a preference for odd-symmetry stimulus compared with the even-symmetry stimulus.

Unexpectedly, V3A (Fig. 3, middle row; considered part of the dorsal pathway) also showed a stronger preference for congruent patterns and for odd symmetry for equiluminant stimuli. This pattern of results was not only characteristic of V3A but was also typical of the other dorsal visual areas, CIP, TOS and dLO, all showing a significant first-harmonic modulation of the BOLD signal for the

chromatic as well as for the luminance stimuli (bootstrap sign-test:  $P < 0.05$ ; Fig. 4).

The equiluminance point was established for each scan and subject by flicker-photometry inside the scanner, and the area of the stimuli was restricted to central vision to minimise contamination of non-equiluminant eccentric stimulation. Nevertheless, the modulation of activity to chromatic stimuli along the dorsal pathway could result from an erroneous equiluminance point or luminance contamination.



To control for this possible artifact, we measured the BOLD response change to random- against congruent-phase stimuli modulated in colour at different red : green colour ratios.

Figure 5 shows how the amplitude and phase of the response modulation to random vs. congruent phase stimuli varied as a function of the red : green colour ratio. The response modulation was present and reliable in both V3A and V4 for all colour ratios. Hence, an error in defining the subjective equiluminance point (corresponding to the outlined number on the abscissa) could not have affected the results. We conclude that the dorsal response modulation to coloured stimuli was not an artifact of an erroneous definition of the equiluminance point.

## Discussion

In this experiment we measured BOLD selectivity to patterns modulated in luminance and chromatic contrast, with different phases but matched amplitude spectra. We observed strong activity modulation in associative areas, particularly in the dorsal pathways, and little or no change in activity in V1 in response to the colour-modulated stimuli.

### Phase selectivity for V1

Confirming the previous study of Perna *et al.* (2008), our results show that alternation between coherent- and random-phase stimuli modulated in luminance activated several areas. The luminance BOLD response to stimuli with different phase congruencies was present in V1, even for the foveal representation. The V1 activity is strictly limited within the borders defining the central 7°, excluding the possibility that it originated from the luminance-colour contrast variation along the external contour of the patch itself. This result reinforces the previous data by Perna *et al.* (2008), who used full-screen stimuli and extend them to a lower range of spatial frequencies. Perna *et al.* (2008) demonstrated that this activity was not due to a greater attentional allocation to the congruent-phase stimuli, given that performing a demanding foveal attentional task did not alter the BOLD modulation in V1, dLO or CIP. The presence of a reliable second-harmonic response in V1 also does not support the attentive explanation.

Perna *et al.* (2008) simulated the BOLD response to random- vs. congruent-phase alternation considering the responses of a battery of neurons with even and odd RFs. In this simple model the pooling of all neuronal activity across space could vary from linear to highly nonlinear combinations. To simulate the stronger response to congruent-phase stimuli, the individual responses needed to be summed after a power amplification with an exponent of 3. A linear summation would produce a small response favouring the random, and an exponent of 2 a well-balanced response.

When the stimuli were modulated in colour, random- against congruent-phase stimuli did not produce any activity change in V1, suggesting that the primary visual area does not discriminate between colour-contrast stimuli of different phase congruencies. This suggests that both local and global RMS colour-contrast are good estimates of the V1 neuronal response: the response varies linearly with RMS contrast. Much evidence demonstrates that the response to equiluminant patterns is more linear (Kaplan & Shapley, 1986), and that in general P-neurons have a linear response to equiluminant grating but not to luminance-modulated gratings. Similarly, VEPs to equiluminant stimuli do not show strong automatic contrast gain-control mechanisms (Morrone *et al.*, 1993), and the present data support this electrophysiological evidence. Importantly, the BOLD

response to colour is nearly linear in V1 (Liu & Wandell, 2005) but becomes more exponential, or saturated, in higher associative areas. In agreement with the present results, this would indicate the presence of a response in higher associative area to congruent vs. random phase stimuli.

It is always difficult to infer a lack of response modulation from the failure to record reliable BOLD signals. However, the fact that from the same stimuli we were able to record a reliable response change at each transition (second-harmonic modulation) suggests that our technique was sensitive enough to detect even small signals, and therefore supports the idea that V1 average activity is invariant to phase manipulation of chromatic stimuli.

We also observed a lack of a response modulation of V1 to different congruent-phase stimuli when modulated in colour. This also indicates that the critical parameter that modulates the response is not the Michelson contrast but the RMS contrast. Indeed, even- and odd-symmetry patterns differ by more than a factor five in Michelson contrast, with random-phase stimuli in between, but the V1 responses were unaffected by this variation.

Symmetry is a property encoded in the phase spectra, in particular in the relationship between the phases of the various harmonics. Boundaries that demarcate an object are associated with changes in contrast, and have odd symmetry; these are points where harmonics of various frequencies have the same phase alignment of  $\pm 90^\circ$ . Conversely, bars are locally even-symmetric functions and correspond to points where the phases of the harmonic components are  $0^\circ$  or  $180^\circ$  (for bright and dark polarity respectively). The responses of neurons with odd-symmetric receptive fields will be stronger to edges than to lines. *Vice versa*, the response of neurons with even-symmetric receptive fields will be stronger to lines than to edges.

The second-harmonic response to the alternation of even- against odd-symmetry stimuli in V1, even for the near-foveal representation, suggests the existence of different neuronal mechanisms with different RF symmetries, some that respond preferentially to lines and the others to edges. The second-harmonic response could result from the adaptation of even- or odd-symmetric RFs neurons. The two different subpopulations of neurons may be present in equal numbers in the same voxel, and the repeated presentation of the neurons' preferred stimulus (which led to response suppression) would elicit a transient response by the unadapted neurons to the complementary stimulus.

In our experiment, the repetition within each block of the odd-symmetry stimulus could adapt the subpopulation of neurons with odd-symmetry RFs, leading to a response, in the following block, to the presentation of the even-symmetry stimulus mediated by neurons with even-symmetry RFs. The V1 BOLD second-harmonic modulation strongly suggests the existence of two subpopulations of chromatic neurons with even- and odd-symmetry RFs, with an overall balanced response.

This is in agreement with a recent electrophysiological study on monkeys (Johnson *et al.*, 2008) that demonstrated the existence of double-opponent cells with oriented receptive fields of various symmetries, equally selective to colour- and luminance-oriented gratings. These types of detectors could perform a 'conjunction analysis' of the chromatic and shape information.

The existence of detectors with different RF symmetries can be inferred from several previous psychophysical studies: colour and luminance phase discrimination is similar once the stimuli are equated for cone contrast (Burr *et al.*, 1989, 1992; Girard & Morrone, 1995; Martini *et al.*, 1996). Taken together, these provide evidence to suggest that for colour, as for luminance, the brain may implement similar algorithms to segment and locate salient features.

### Phase selectivity for dorsal and ventral associative areas

All our stimuli, modulated either in luminance or in colour, elicited widespread modulation of activity in V3A, in dorsal LO, in the more caudal part of the occipital branch of the intraparietal sulcus, in TOS and in V4. The responses in these areas showed a preference for congruent-phase stimuli and for odd-symmetry stimuli, both for luminance and for colour. These higher cortical areas are involved both in the phase-congruency computation (given the small response to noise) and also in the computation of absolute phases (given the preference for odd-symmetry), suggesting a role in contour detection. Contours are associated with the phase congruency of  $\pm 90^\circ$ , and are more frequent in natural images than other features. It is possible that at higher levels of analysis the neurons that locally process contours are more numerous, eliciting a stronger BOLD response. This conclusion supports previous fMRI studies that found V3A, V4 and LO to be active during contour processing (Schira *et al.*, 2004) and dLO, CIP and TOS to be involved in brightness perception of surfaces (Perna *et al.*, 2005; Cornelissen *et al.*, 2006). However, we cannot dismiss the possibility that the stronger BOLD response to the checkerboard pattern may also be generated by the presence of the brightness illusion that increases the saliency of the pattern.

Unexpectedly, our results demonstrate that the dorsal pathway is involved as much as the ventral pathway in detecting salient features modulated in colour. The dorsal involvement in the analysis of colour is at odds with the traditional view that assigns colour analysis to only the ventral pathway while shape analysis may also involve the dorsal pathway (for a review see Grill-Spector & Malach, 2004). However, in many natural conditions, contours are associated with changes both in chromatic and in luminance contrast (Hansen & Gegenfurtner, 2009). To detect the surface contour it would be more efficient to analyse the luminance and the chromatic information together. It is possible that the analysis performed by the dorsal pathway conveys the contour signals that mediate action towards equiluminant shapes, which has been demonstrated to be as reliable as for luminance-contrast stimuli.

Responses in the dorsal pathway to colour stimuli have been observed by many authors (Liu & Wandell, 2005; Mullen *et al.*, 2010; D'Souza *et al.*, 2011) and the responses in these areas are similar for luminance and colour stimuli, as we observed here. At present it is still unclear whether these areas form part of the cerebral network specialised for colour perception, and the strong V3A activation to chromatic stimuli observed in our study does not imply that this and other dorsal areas mediate colour perception, but that they are involved in the analysis of colour form.

As for luminance, it seems that chromatic-contrast detectors operating as early as V1 may be selective for spatial phase. However, preference for edge-like phase takes place only in areas downstream of V1, in the higher-order visual areas. The role of V4 seems not to be crucial, but only part of a network for the analysis of colour form: a stronger response to edges indicates that odd-symmetric RFs may be more common or more sensitive in V4.

### Conclusions

In conclusion, the human visual system seems to possess the mechanisms needed to analyse colour and form together, as a single attribute of an image, in order to structure the representation of the visual scene. This fMRI study demonstrates that both the dorsal and ventral pathways are involved in colour-form analysis, which could be based on selectivity to spatial phase.

### Acknowledgements

We thank Giovanni D'Avossa and Mark McAvoy for help in installing and running the 4DFP software kindly provided by University of Washington, St Louis. We also thank Marco Cicchini for help in programming, gamma calibrating and cone-contrast calculation of the stimuli. This work was supported by the EC project STANIB (FP7-ERC) and PRIN 2010 by the MIUR. E.C. was supported by a fellowship from the University of Florence. The authors declare no potential conflict of interest, financial or otherwise.

### Abbreviations

BOLD, blood oxygen level-dependent; CIP, caudal part of the intraparietal sulcus; dLO, dorsal lateral occipital complex; fMRI, functional magnetic resonance imaging; RF, receptive field; RMS, root-mean-square; RoI, region of interest; STS, superior temporal sulcus; TOS, transversal occipital sulcus; V1, primary visual cortex (V1); VEP, visual evoked potential.

### References

- d'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D.C. & Morrone, M.C. (2007) Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nat. Neurosci.*, **10**, 249–255.
- Bell, A.J. & Sejnowski, T.J. (1997) The “independent components” of natural scenes are edge filters. *Vision Res.*, **37**, 3327–3338.
- Brainard, D.H. (1997) The Psychophysics Toolbox. *Spatial Vision*, **10**, 433–436.
- Burr, D.C., Morrone, M.C. & Spinelli, D. (1989) Evidence for edge and bar detectors in human vision. *Vision Res.*, **29**, 419–431.
- Burr, D.C., Morrone, M.C. & Fiorentini, A. (1992) Electro-physiological investigation of edge-selective mechanisms of human vision. *Vision Res.*, **32**, 239–247.
- Cornelissen, F.W., Wade, A.R., Vladusich, T., Dougherty, R.F. & Wandell, B.A. (2006) No functional magnetic resonance imaging evidence for brightness and colour filling-in in early human visual cortex. *J. Neurosci.*, **26**, 3634–3641.
- Crespi, S., Biagi, L., d'Avossa, G., Burr, D.C., Tosetti, M. & Morrone, M.C. (2011) Spatiotopic coding of BOLD signal in human visual cortex depends on spatial attention. *PLoS One*, **6**, e21661.
- D'Souza, D.V., Auer, T., Strasburger, H., Frahm, J. & Lee, B.B. (2011) Temporal frequency and chromatic processing in humans: an fMRI study of the cortical visual areas. *J. Vision*, **11**, 1–17.
- Efron, B.T. & Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. Chapman and Hall, New York.
- Engel, S.A. & Furlanski, C.S. (2001) Selective adaptation to colour contrast in human primary visual cortex. *J. Neurosci.*, **21**, 3949–3954.
- Engel, S.A., Glover, G.H. & Wandell, B.A. (1997) Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cereb. Cortex*, **7**, 181–192.
- Felsen, G., Touryan, J., Han, F. & Dan, Y. (2005) Cortical sensitivity to visual features in natural scenes. *PLoS Biol.*, **3**, e342.
- Field, D.J. & Tolhurst, D.J. (1986) The structure and symmetry of simple-cell receptive-field profiles in the cat's visual cortex. *P. Roy. Soc. Lond. B Bio.*, **228**, 379–400.
- Gaska, J.P., Pollen, D.A. & Cavanagh, P. (1987) Diversity of complex cell responses to even- and odd-symmetric luminance profiles in the visual cortex of the cat. *Exp. Brain Res.*, **68**, 249–259.
- Girard, P. & Morrone, M.C. (1995) Spatial structure of chromatically opponent receptive fields in the human visual system. *Visual Neurosci.*, **12**, 103–116.
- Grill-Spector, K. & Malach, R. (2004) The human visual cortex. *Annu. Rev. Neurosci.*, **27**, 649–677.
- Hadjikhani, N., Liu, A.K., Dale, A.M., Cavanagh, P. & Tootell, R.B. (1998) Retinotopy and colour sensitivity in human visual cortical area V8. *Nat. Neurosci.*, **1**, 235–241.
- Hansen, K.A., Kay, K.N. & Gallant, J.L. (2007) Topographic organization in and near human visual area V4. *J. Neurosci.*, **27**, 11896–11911.
- Hansen, T. & Gegenfurtner, K.R. (2009) Independence of colour and luminance edges in natural scenes. *Visual Neurosci.*, **26**, 35–49.
- Henriksson, L., Hyvarinen, A. & Vanni, S. (2009) Representation of cross-frequency spatial phase relationships in human visual cortex. *J. Neurosci.*, **29**, 14342–14351.
- Hubel, D.H. & Wiesel, T.N. (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.*, **160**, 106–154.

- Johnson, E.N., Hawken, M.J. & Shapley, R. (2008) The orientation selectivity of colour-responsive neurons in macaque V1. *J. Neurosci.*, **28**, 8096–8106.
- Jones, J.P., Stepnoski, A. & Palmer, L.A. (1987) The two-dimensional spectral structure of simple receptive fields in cat striate cortex. *J. Neurophysiol.*, **58**, 1212–1232.
- Kaplan, E. & Shapley, R.M. (1986) The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. *Proc. Natl. Acad. Sci. USA*, **83**, 2755–2757.
- Kleinschmidt, A., Lee, B.B., Requardt, M. & Frahm, J. (1996) Functional mapping of colour processing by magnetic resonance imaging of responses to selective P- and M-pathway stimulation. *Exp. Brain Res.*, **110**, 279–288.
- Liu, J. & Wandell, B.A. (2005) Specializations for chromatic and temporal signals in human visual cortex. *J. Neurosci.*, **25**, 3459–3468.
- Martini, P., Girard, P., Morrone, M.C. & Burr, D.C. (1996) Sensitivity to spatial phase at equiluminance. *Vision Res.*, **36**, 1153–1162.
- McDonald, J.S., Mannion, D.J., Goddard, E. & Clifford, C.W. (2010) Orientation-selective chromatic mechanisms in human visual cortex. *J. Vision*, **10**, 34.
- Mechler, F., Reich, D.S. & Victor, J.D. (2002) Detection and discrimination of relative spatial phase by V1 neurons. *J. Neurosci.*, **22**, 6129–6157.
- Mechler, F., Ohiorhenuan, I.E. & Victor, J.D. (2007) Speed dependence of tuning to one-dimensional features in V1. *J. Neurophysiol.*, **97**, 2423–2438.
- Morgan, M.J., Ross, J. & Hayes, A. (1991) The relative importance of local phase and local amplitude in patchwise image reconstruction. *Biol. Cybern.*, **65**, 113–119.
- Morrone, M.C. & Burr, D.C. (1988) Feature detection in human vision: a phase-dependent energy model. *P. Roy. Soc. Lond. B Bio.*, **235**, 221–245.
- Morrone, M.C. & Burr, D.C. (1997) Capture and transparency in coarse quantized images. *Vision Res.*, **37**, 2609–2629.
- Morrone, M.C., Burr, D.C. & Fiorentini, A. (1993) Development of infant contrast sensitivity to chromatic stimuli. *Vision Res.*, **33**, 2535–2552.
- Movshon, J.A., Thompson, I.D. & Tolhurst, D.J. (1978a) Receptive field organization of complex cells in the cat's striate cortex. *J. Physiol.*, **283**, 79–99.
- Movshon, J.A., Thompson, I.D. & Tolhurst, D.J. (1978b) Spatial summation in the receptive fields of simple cells in the cat's striate cortex. *J. Physiol.*, **283**, 53–77.
- Mullen, K.T., Dumoulin, S.O., McMahon, K.L., de Zubicaray, G.I. & Hess, R.F. (2007) Selectivity of human retinotopic visual cortex to S-cone-opponent, L/M-cone-opponent and achromatic stimulation. *Eur. J. Neurosci.*, **25**, 491–502.
- Mullen, K.T., Thompson, B. & Hess, R.F. (2010) Responses of the human visual cortex and LGN to achromatic and chromatic temporal modulations: an fMRI study. *J. Vision*, **10**, 13.
- Oلمان, C.A., Ugurbil, K., Schrater, P. & Kersten, D. (2004) BOLD fMRI and psychophysical measurements of contrast response to broadband images. *Vision Res.*, **44**, 669–683.
- Oppenheim, A.V. & Lim, J.S. (1981) The importance of phase in signals. *Proc. IEEE*, **69**, 529–541.
- Perna, A. & Morrone, M.C. (2007) The lowest spatial frequency channel determines brightness perception. *Vision Res.*, **47**, 1282–1291.
- Perna, A., Tosetti, M., Montanaro, D. & Morrone, M.C. (2005) Neuronal mechanisms for illusory brightness perception in humans. *Neuron*, **47**, 645–651.
- Perna, A., Tosetti, M., Montanaro, D. & Morrone, M.C. (2008) BOLD response to spatial phase congruency in human brain. *J. Vision*, **8**, 11–15.
- Piotrowski, L.N. & Campbell, F.W. (1982) A demonstration of the visual importance and flexibility of spatial-frequency amplitude and phase. *Perception*, **11**, 337–346.
- Pollen, D.A. & Ronner, S.F. (1981) Phase relationships between adjacent simple cells in the visual cortex. *Science*, **212**, 1409–1411.
- Pollen, D.A., Gaska, J.P. & Jacobson, L.D. (1988) Responses of simple and complex cells to compound sine-wave gratings. *Vision Res.*, **28**, 25–39.
- Press, W.A., Brewer, A.A., Dougherty, R.F., Wade, A.R. & Wandell, B.A. (2001) Visual areas and spatial summation in human visual cortex. *Vision Res.*, **41**, 1321–1332.
- Rainer, G., Augath, M., Trinath, T. & Logothetis, N.K. (2001) Nonmonotonic noise tuning of BOLD fMRI signal to natural images in the visual cortex of the anesthetized monkey. *Curr. Biol.*, **11**, 846–854.
- Rainer, G., Augath, M., Trinath, T. & Logothetis, N.K. (2002) The effect of image scrambling on visual cortical BOLD activity in the anesthetized monkey. *NeuroImage*, **16**, 607–616.
- Ringach, D.L. (2002) Spatial structure and symmetry of simple-cell receptive fields in macaque primary visual cortex. *J. Neurophysiol.*, **88**, 455–463.
- Ringach, D.L. (2004) Mapping receptive fields in primary visual cortex. *J. Physiol.*, **558**, 717–728.
- Schira, M.M., Fahle, M., Donner, T.H., Kraft, A. & Brandt, S.A. (2004) Differential contribution of early visual areas to the perceptual process of contour processing. *J. Neurophysiol.*, **91**, 1716–1721.
- Schluppeck, D. & Engel, S.A. (2002) Colour opponent neurons in V1: a review and model reconciling results from imaging and single-unit recording. *J. Vision*, **2**, 480–492.
- Sereno, M.I., Dale, A.M., Reppas, J.B., Kwong, K.K., Belliveau, J.W., Brady, T.J., Rosen, B.R. & Tootell, R.B. (1995) Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, **268**, 889–893.
- Spitzer, H. & Hochstein, S. (1985) A complex-cell receptive-field model. *J. Neurophysiol.*, **53**, 1266–1286.
- Sumner, P., Anderson, E.J., Sylvester, R., Haynes, J.D. & Rees, G. (2008) Combined orientation and colour information in human V1 for both L-M and S-cone chromatic axes. *NeuroImage*, **39**, 814–824.
- Talairach, J. & Tournoux, P. (1988) *Co-Planar Stereotaxic Atlas of the Human Brain*. Thieme Medical Publishers, New York.
- Tjan, B.S., Lestou, V. & Kourtzi, Z. (2006) Uncertainty and invariance in the human visual cortex. *J. Neurophysiol.*, **96**, 1556–1568.
- Tootell, R.B. & Hadjikhani, N. (2001) Where is 'dorsal V4' in human visual cortex? Retinotopic, topographic and functional evidence. *Cereb. Cortex*, **11**, 298–311.
- Wade, A.R., Brewer, A.A., Rieger, J.W. & Wandell, B.A. (2002) Functional measurements of human ventral occipital cortex: retinotopy and colour. *Philos. T. Roy. Soc. B.*, **357**, 963–973.
- Wandell, B.A., Brewer, A.A. & Dougherty, R.F. (2005) Visual field map clusters in human cortex. *Philos. T. Roy. Soc. B.*, **360**, 693–707.
- Wichmann, F.A., Braun, D.I. & Gegenfurtner, K.R. (2006) Phase noise and the classification of natural images. *Vision Res.*, **46**, 1520–1529.