Vision Research 89 (2013) 47–53

Contents lists available at SciVerse ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Discomfort and the cortical haemodynamic response to coloured gratings

Sarah M. Haigh, Laura Barningham, Monica Berntsen, Louise V. Coutts, Emily S.T. Hobbs, Jennifer Irabor, Eleanor M. Lever, Peter Tang, Arnold J. Wilkins *

Department of Psychology, University of Essex, Wivenhoe Park, Colchester, Essex CO4 3SQ, UK

ARTICLE INFO

Article history:
Received 22 February 2013
Received in revised form 26 June 2013
Available online 15 July 2013

Keywords:
Chromaticity separation
Near infrared spectroscopy
Discomfort

ABSTRACT

In five experiments we measured the amplitude of the haemodynamic response to visual patterns using near infrared spectroscopy of the visual cortex. The patterns were gratings with bars that differed in chromaticity but not in luminance. In all experiments, with a wide range of chromaticities of the grating bars, the amplitude of the haemodynamic response increased with the separation of the chromaticities in the CIE 1976 UCS diagram. The amplitude did not vary consistently with the cone activation, or with the signal in colour difference channels. In four further experiments, again with a wide range of chromaticities, the gratings were rated for visual comfort. Discomfort increased consistently with the separation of the chromaticities. Given that a large haemodynamic response to patterns is generally associated with headache, we suggest that the discomfort may be a homeostatic signal to reduce sustained metabolic load on the visual cortex.

© 2013 Published by Elsevier Ltd.

1. Introduction

Colour coding in the visual cortex has been the subject of long-standing debate. Several studies have found evidence to suggest that the majority of neurons in the visual cortex respond to luminance contrast more than chromatic contrast (Lennie, Krauskopf, & Sclar, 1990; Ts'o & Gilbert, 1988). Some have found a topographic representation of chromaticity (Xiao, Wang, & Felleman, 2003); whereas others have found a cone-opponent activation (L − M, S − (L + M) and L + M) (Livingstone & Hubel, 1984; Ts'o & Gilbert, 1988; Vautin & Dow, 1985).

When mapping colour representation in the visual cortex, some colour pairs appear to evoke a stronger cortical response than others. Salzmann et al. (2012) used colour opponent flicker (red-green and blue-yellow) and colour-grey flicker (red-grey, green-grey, blue-grey and yellow-grey). They found that the red-green flicker and the red-grey flicker produced the strongest response when identifying the colour blobs in V1 and V2 in the monkey cortex. Tanigawa, Lu, and Roe (2010) also found colour blobs in macaque V4; certain areas of V4 respond more strongly to one colour over another (e.g. magenta-black gratings over blue-black gratings).

Several studies have sought a metric for the cortical activation that occurs in response to chromatic stimuli. Goddard et al. (2010) found greater fMRI BOLD activation for certain cone-opponent channels (namely lime-magenta coloured patterns over orange-cyan patterns), suggesting integration of the cone-opponent channels as early as V1. However, Brouwer and Heeger (2009) found that the transition from cone-opponent colour coding to perceptual colour coding (measured using CIE LAB) began in V1 and was the strongest in V4 and VO1.

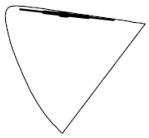
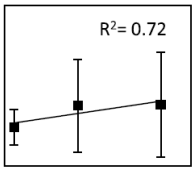
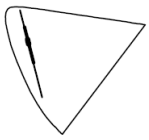
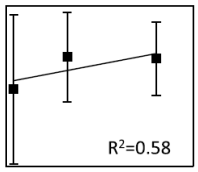
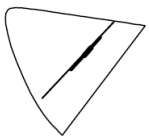
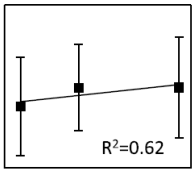
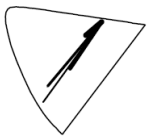
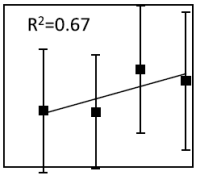
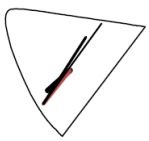
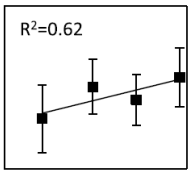
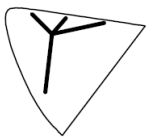
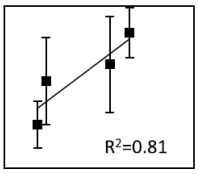
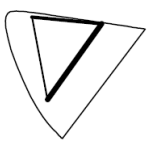
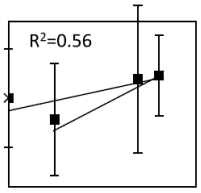
Similarly, Parkes et al. (2009) measured the fMRI BOLD responses to flickering radial patterns that were composed of either cone-opponent cardinal colours (red-green or lime-violet), or perceptual colours that were chosen to be equally discriminable (red, green, yellow, blue). For the cardinal colours, the lime-violet pattern evoked a larger BOLD response than the red-green pattern, but not significantly so. The perceptual colours evoked BOLD responses that were similar to one another, even though the individual differences in the BOLD response to each perceptual colour pattern were reliable enough to predict the colour viewed, suggesting that colour organisation in the cortex is not based on cone-activation, but on a more perceptual representation.

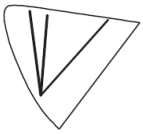
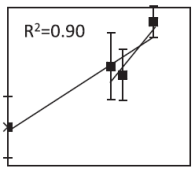
Mullen et al. (2007) measured the fMRI BOLD response in the visual cortex to radial chromatic red/green and yellow/blue grating patterns that differed either (1) in cone activation, or (2) in multiples of detection threshold. The amplitude of the BOLD response was not linearly related to either measure.

Laeng, Hugdahl, and Specht (2011), however, measured the BOLD response in patients with synaesthesia when viewing chromatic letters and when seeing illusory colours. They measured the colour difference between the real and illusory colours (in RGB and CIExyY colour spaces) and found that there was a correlation between the BOLD activation and the colour difference

* Corresponding author. Fax: +44 (0)1206 873801.
E-mail address: arnold@essex.ac.uk (A.J. Wilkins).

Table 1
The grating colours described in words and in terms of their CIE UCS 1976 chromaticity coordinates. The coordinates are shown by the ends of lines in the inset CIE UCS diagra
Where superposed, the lines vary in thickness. The amplitude of the haemodynamic response is shown as a function of the separation of the chromaticities of the grating ba
with the R^2 values of the slopes. In Experiments 4 and 5 a black–white grating was included in the regression. Separate regressions are shown without the data for these gratin
Error bars show standard deviations.

Experiment	Description	Chromaticity coordinates: first colour u'	first colour v'	second colour u'	second colour v'	CIE UCS diagram	NIRS amplitude
1a	Orangey yellow - greeny yellow	0.25	0.55	0.28	0.55		
	Orange – yellowy green	0.37	0.54	0.17	0.56		
	Red – green	0.48	0.52	0.07	0.57		
1b	Greeny turquoise – blueish turquoise	0.11	0.42	0.10	0.44		
	Turquoisey green – turquoisey blue	0.13	0.34	0.09	0.50		
	Green- blue	0.07	0.57	0.17	0.18		
1c	Reddish purple - bluish purple	0.38	0.41	0.35	0.37		
	Purplish red - purplish blue	0.43	0.46	0.29	0.31		
	Red-blue	0.48	0.52	0.17	0.18		
2a	Red – reddish purple	0.43	0.52	0.36	0.46		
	Red – purple	0.43	0.52	0.29	0.31		
	Red - purple/blue	0.43	0.52	0.19	0.23		
	Red – blue	0.43	0.52	0.17	0.16		
2b	Purple - purple/blue	0.29	0.31	0.19	0.22		
	Blue – purple	0.17	0.16	0.29	0.31		
	Blue - red/purple	0.17	0.16	0.36	0.46		
	Red – blue	0.43	0.52	0.17	0.16		
3	Red-grey	0.44	0.52	0.21	0.47		
	Blue-grey	0.18	0.21	0.21	0.47		
	Green-grey	0.12	0.56	0.21	0.47		
	Yellow-grey	0.27	0.54	0.21	0.47		
4	Red-blue	0.43	0.53	0.19	0.19		
	Red-green	0.43	0.53	0.12	0.56		
	Blue-green	0.19	0.19	0.12	0.56		
	White-black	0.20	0.48	0.20	0.48		

Experiment	Description	Chromaticity coordinates: first colour u'	first colour v'	second colour u'	second colour v'	CIE UCS diagram	NIRS amplitude
5	Red-blue	0.48	0.52	0.17	0.17		
	Yellow-blue	0.20	0.54	0.17	0.17		
	Green-blue	0.12	0.56	0.17	0.17		
	White-black	0.20	0.48	0.20	0.48		

calculated using either colour space. Given this finding and the topographic representation of chromaticity reported by Xiao, Wang, and Felleman (2003) it is possible that cortical activation by two colours is related to the difference in their chromaticity in some way.

In the present study we recorded the cortical haemodynamic response to chromatic grating patterns using near infrared spectroscopy (NIRS). NIRS measures the relative change in oxyhaemoglobin and deoxyhaemoglobin responses, which are negatively correlated. The deoxyhaemoglobin response is more closely correlated to the BOLD response than the oxyhaemoglobin response (MacIntosh, Klassen & Menon, 2003; Toronov et al., 2001). However, the signal to noise ratio for the deoxyhaemoglobin response is much smaller than the oxyhaemoglobin signal (Strangman, Culver, Thompson & Boas, 2002), and so, in the present study, only the oxyhaemoglobin response will be reported. NIRS has poorer spatial resolution than fMRI and can give a reflection of the activation of the visual cortex but not the activation within a specific visual area.

We show that the amplitude of the oxyhaemoglobin response is not consistently related to the extent of activation of the cones or of the colour opponent channels. However, when the difference between the grating bars is expressed in terms of the separation between their chromaticities in the CIE 1976 UCS diagram, a simple relationship with the amplitude of the haemodynamic response emerges. The relationship holds for a wide range of hues.

2. Experiments 1–5

2.1. Methods

The participants were students from the University of Essex: 30 in Experiment 1, seven in Experiment 2, nine in Experiment 3 six in Experiment 4, and seven in Experiment 5. All participants were aged 18–48. None had a history of seizures. In Experiment 1, all participants had a minimum acuity of 6/6 monocularly and binocularly (Lighthouse Near and Far tests of visual acuity) and a minimum stereoacuity of 60 s arc (Titmus test). Log contrast sensitivity for letters was at least 2.00 (Pelli-Robson letter chart), and no colour deficiencies were detected (Ishihara plates). In Experiment 1 three were wearing contact lenses during the study.

2.1.1. Stimuli

Horizontal gratings were displayed on a 24″ LCD Dell screen with a backlight refresh rate of 163 Hz. In Experiment 1, the three extremes of the screen gamut (red pixels only, green only or blue only) were measured using a telespectroradiometer (Model PR-670®, Photo Research®, Chatsworth, CA, USA). The midpoints between pairs of each of the three extremes (red–green, green–blue and blue–red) were calculated. Chromaticities equidistant from either side of each midpoint were then used in alternating stripes to create three grating patterns involving a separation of chromaticities in the CIE 1976 UCS diagram. The separation was small (mean 0.03), medium (mean 0.19) or large (mean 0.43). On the red-green (RG) axis the gratings had the following colour pairs: orange–greenish yellow, reddish orange–yellowy green, red–green. On the green–blue (GB) axis they had the following colour pairs: greenish turquoise–bluish turquoise, turquoisy green–turquoisy blue, green–blue, and on the red-blue axis (RB): reddish purple–bluish purple, purplish red–purplish blue, red–blue. Table 1 gives the chromaticities, and they are represented by the ends of the thick, medium and thin lines in the inset CIE 1976 UCS diagrams. The stripes all had a luminance of 29 cd m^{-2}. The spatial frequency of the patterns was 2 cycle deg^{-1} (cpd) at a viewing distance of 1 m, and the patterns were circular in outline. A black central fixation cross subtending 1.3° of visual angle was shown throughout the trial.

The conditions were broadly similar in Experiments 2–5, although they varied slightly as we gathered experience with the techniques of NIRS measurement. The colour of the gratings differed as shown in Table 1. The colour-pairs and their chromaticities used in each experiment are listed, and shown by the ends of the lines in the CIE 1976 UCS diagrams. The spatial frequency of the grating patterns was between 1.36–1.70 cpd and the patterns were square in outline. In addition to the coloured gratings, Experiments 4 and 5 contained a single achromatic grating.

All the gratings used had a square-wave luminance profile. Square-wave gratings were used instead of sinusoidal gratings to ensure that any effects of the colour-pairs were not due to problems in accommodating on the target. Square-wave gratings may provide a better target for accommodation than sine-wave gratings (O'Hare & Hibbard, 2013), and gratings between 2–8 cpd provide strong retinal contrast (MacKenzie, Hoffman, & Watt, 2010). Haigh et al. (2013) used gratings similar to those in Experiment 1. They showed that accommodation was unaffected by the difference in chromaticity between the colour-pairs when displayed in a 2 cpd square-wave grating with similar luminance.

In all experiments the gratings subtended 10 deg, and were surrounded by a grey field of similar luminance. In all experiments the bars of the coloured gratings had the same (photometric) luminance, although the space-averaged luminance varied between

experiments from 14 to 22 cd m^{-2}. The gratings were presented for 10–16 s and were repeated 4–8 times. A grey screen was presented between each grating for 30 s and, for Experiments 2–5, a central fixation cross was presented for 1 s immediately before stimulus presentation. Experiment 2 was conducted in two immediately successive sessions using different chromaticities which were analysed separately, shown in Table 1 as 2a and 2b.

2.1.2. Procedure

The haemodynamic response was measured using an 8-channel near infrared spectroscopy (NIRS) system (Oxymon Mk II Artinis Medical Systems BV Zetten, Netherlands). A photodiode and associated electronics was used as a trigger for the NIRS system. The optode placement used in Experiment 1 is shown on the left in Fig. 1. Two receivers were placed symmetrically 20 mm above the inion and 30 mm either side of the midline. Two transmitters were then placed vertically 30 mm from the receiver, covering O1 and O2 (10–20 system for electrode placement). Three more transmitters were then placed laterally around each of the receivers at 40° intervals with a radius of 30 mm from the receiver. Previous studies (Coutts et al., 2012) have used NIRS to investigate the haemodynamic response to aversive monochrome gratings. Given the possibility that the aversion might change blood pressure, the pressure was transduced continually. In the event, no changes in blood pressure were associated with stimulus presentation. Nevertheless in Experiment 1 the frontal channels were included as a further control for systemic effects. They showed little response and were not used in Experiments 2–5, which included a fourth posterior channel each side, positioned as described by Coutts et al. (2012) and shown in Fig. 1.

The stimuli were presented for 16 s to allow the haemodynamic response to reach its maximum. The order of the stimuli was randomized and each pattern was presented twice, but never in immediate succession. Each trial began with a grey screen. The grey screen separated each stimulus presentation and lasted for an interval that varied randomly between 27 and 36 s with a uniform probability distribution. This interstimulus interval was sufficient to allow any effects of colour adaptation to subside and to allow the NIRS signal to return to baseline. The participants viewed the stimuli binocularly in a darkened room from a distance of 1 m.

2.1.3. Data analysis

A differential path length factor of 6.26 was used for the calculation of oxygenated haemoglobin concentrations in μmolar units (Duncan et al., 1996). The data were analysed using MATLAB (The MathWorks Inc., Natick, MA), using the Signal Processing Toolbox™. Deoxygenated haemoglobin (Hhb) responses were smaller, but negatively correlated with the oxygenated haemoglobin (HbO_2) responses, and were not analysed. The near infrared signal was filtered using a low-pass 5th order Butterworth filter with a cut off frequency of 0.667 Hz to remove cardiac artefact.

In Experiment 1, to measure the response to the grating, the baseline response (an average of the response before stimulus onset and after stimulus offset) was subtracted from the peak response (during stimulus presentation). The baseline was calculated from the response 9 s before stimulus onset for a period of 5 s, and from the response 10 s after stimulus offset for a period of 5 s. The peak response was calculated from the signal 6 s after stimulus onset for a period of 10 s. This corrected for any drift of the signal.

In Experiment 1 two criteria were used to ensure signal quality. If the channel returned an unvarying signal for more than 5% of the recording time (suggesting that the signal was obscured by hair) then the channel was excluded (Criterion 1). For each channel and each participant we averaged the signal for all stimuli and calculated the difference between the peak signal and baseline. We expressed this as a ratio of the standard deviation of the signal 10 s before stimulus onset. If this ratio was less than 1, then the channel was rejected (Criterion 2). Following the above criteria, an average of 3.8 posterior channels from 16 participants were accepted for analysis and were averaged separately for each participant and stimulus. Only two participants had frontal channels which passed both criteria.

Note that because near infrared spectroscopy has poor spatial resolution the functioning channels were highly correlated.

2.2. Results

For an initial analysis of the data from Experiment 1 only channels which failed Criterion 1 were excluded. An independent samples *t*-test compared the effect of the position of the optode (frontal or posterior) on the magnitude of the oxyhaemoglobin response. There was a main effect of optode position ($t(120.7) = 5.26$, $p < .001$); the posterior optodes producing a stronger response to the stimuli. The remaining analyses were confined to those channels that satisfied both Criterion 1 and Criterion 2 described previously.

For the posterior optodes, a repeated-measures analysis of variance with the colour pair (RG, GB or RB) as the main effect, showed no effect of the colour pair ($F(2,30) = 1.30$, $p = .289$). A repeated-measures analysis of variance with the colour separation as a main effect found a significant effect of the colour separation ($F(2,30) = 4.32$, $p = .022$), attributable to the difference between the small colour separation and the remainder. The mean oxyhaemoglobin response for each colour separation for the posterior channels is shown in Fig. 2. The small signal in the frontal channels did not justify such an analysis.

The patterns with the largest chromaticity separation produced the largest change in the haemodynamic response and there was no significant change in frontal channels. In the next four experiments, the haemodynamic response was therefore measured only in posterior channels. The averaging periods used to calculate the amplitude of the response varied slightly from one study to another but included the period immediately before stimulus presentation and the last 8 s of stimulus presentation.

For Experiments 2–5, there was an increase in the oxyhaemoglobin response with colour separation, as was the case in Experiment 1 (see Fig. 2). A Page's L test (Page, 1963) was used to test the significance of the tendency across all five experiments for the amplitude of the oxyhaemoglobin response to increase with CIE UCS colour separation. The increase was significant across experiments ($\rho(1) = 9.60$, $p < .002$), but not for each experiment individually.

In all five experiments (8 cases) the change in oxygenation consequent upon the presentation of the grating increased with the

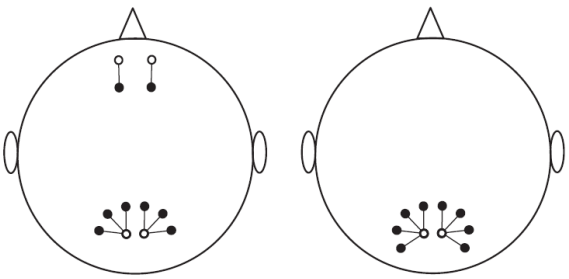


Fig. 1. The montage for the NIRS optode placement. The grey circles represent the transmitters and white circles the receivers. Lines represent the channels. Left: Experiment 1; right: Experiments 2–5.

separation in the chromaticity of the two component bars in the grating: i.e. the correlation was positive in all 8 cases irrespective of hue angle. In contrast, the energy captured by the three cone classes and the chromatic visual channels did not show any consistent trends, as can be seen from Table 2 in which the bold figures show positive correlations. This suggests that the amplitude of the haemodynamic response is not directly based on cone or channel activation, but more on perceptual colour difference.

Cone activation was calculated using the colour coordinates from the CIE XYZ colour space according to the following formulae taken from Hunt (1991):

$$\text{L cone} = 0.38971 * X + 0.68898 * Y - 0.07868 * Z$$
$$\text{M cone} = -0.22981 * X + 1.1834 * Y + 0.04641 * Z$$
$$\text{S cone} = Z$$

3. Discussion

The minimum chromaticity separation was more than five times the threshold separation at which the difference was just discernible in a 2 deg field (McAdam, 1981). Nevertheless the haemodynamic response consistently increased with chromaticity separation, and did so for a wide variety of hues. Although the S stimuli have higher contrast thresholds at 2 cpd and may have been less visible than the other hues, the simple relationship with chromaticity separation was maintained.

Mullen et al. (2007) related the fMRI BOLD response to gratings that varied in (1) cone activation, and, (2) multiples of detection threshold on the two cone-opponent pathways (long- and medium–wavelength (L–M) and short-wavelength (S)-cone-opponent) and on the achromatic pathway. The BOLD amplitude was not well predicted by threshold-scaled stimuli but was better predicted by cone contrast, particularly for area V1. Their coloured stimuli did not vary on more than one opponent pathway, however. The present findings suggest that when stimulation involves simultaneous variation in more than one opponent pathway, the haemodynamic response may be related to the perceptual difference in colour independent of the cone contrast, at least when the grating bars have similar luminance.

The BOLD responses reported by Parkes et al. (2009) show a larger amplitude from the lime-violet patterns than the red-green patterns (although this was not significant). There were no differences in the amplitude of the BOLD responses from the perceptual-coloured patterns (red–grey, green–grey, yellow–grey and blue–grey). All colours were isoluminant. When the separation of CIE UCS chromaticity for all their patterns was calculated, the difference in chromaticity between the perceptual colours and grey were similar (mean = 0.04, se = 0.01), whereas the lime-violet pattern had a larger chromaticity separation (0.12) compared to the red-green pattern (0.08). Again, this suggests that it is the chromaticity separation which drives the larger haemodynamic responses in primary visual cortex (V1).

Goddard et al. (2010) reported that there was a cortical bias (in terms of the strength of the fMRI response) for their lime-magenta colours than for their orange-cyan. These authors kindly made their chromaticities available, and, when cone activation was converted into CIE 1976 UCS there was a larger chromaticity separation between lime and magenta pairs than orange and cyan. When the differences in luminance were taken into account using CIELUV, the colour difference (delta E^*) was larger for the two lime and magenta pairs than the two orange and cyan (357 and 364 versus 426 and 400 respectively), again suggesting that the uniform perceptual space is important in predicting the cortical activation.

Similarly, when the CIE xyY chromaticities used by Salzmann et al. (2012) were converted to CIE 1976 UCS colour space, the red-green alternating flicker had the largest chromaticity separation (0.33), and produced the clearest signals, compared to the blue-yellow flicker (0.26) which produced much weaker signals. The chromaticity separation may explain part of the variability in 'blob' detection in response to chromatic flicker.

Laeng, Hugdahl, and Specht (2011) also found a correlation between fMRI BOLD activation and colour difference, although in synaesthetes. They measured the colour difference in a perceptually non-uniform colour space (RGB and xyY). The correlation might have been larger had the space been perceptually uniform.

In the current study, we have found a linear relationship between the amplitude of the oxyhaemoglobin response and colour difference when measured using a uniform colour space (CIE 1976 UCS). The average slope of the function was 0.23 micromolar. Note that this value lies within the 95% confidence limits of all the functions shown in Table 1.

Xiao, Wang, and Felleman (2003) found that colour coding in V2 in the macaque had the same spatial organisation as the DIN colour map (a perceptual colour map similar to the CIE 1976 UCS diagram). A proportion of inhibitory connections in the visual cortex are local (McDonald & Burkhalter, 1993; Stepanyants et al., 2009). The presence of topographic maps of chromaticity in V2 suggests that gratings with a large colour difference might be exciting neurons with a large spatial separation within the cortical network. Given that cortical inhibition is local, we might speculate that the larger haemodynamic response is a reflection of the lower inhibition associated with spatially disparate excitation.

The prolonged presentation duration (16 s) may have created after-effects after stimulus-offset. This, however, should not have affected the calculation of the amplitude of the oxyhaemoglobin response because any baseline post-response began at least 4 s

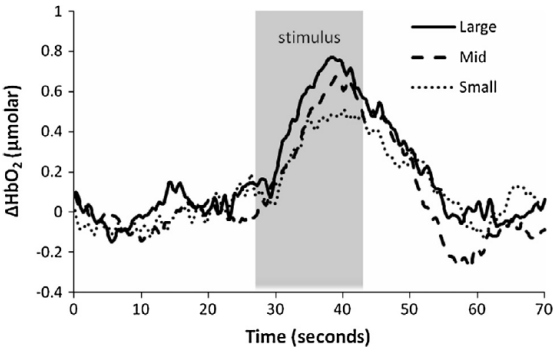


Fig. 2. The mean change in HbO_2 in the posterior channels for the patterns with large, medium and small separation of chromaticity, averaged over the three colour pairs in Experiment 1.

Table 2
Correlations between the amplitude of the oxyhaemoglobin response and various measures of stimulus energy shown as Pearson product moment coefficients. The oxyhaemoglobin response in Experiment 1 was analysed separately for each colour pair. Positive values are shown in bold.

Experiment	L cone	M cone	S cone	L – M	S – (L + M)	UCS
1a	**0.90**	**0.27**	**0.65**	**0.34**	**0.66**	**0.73**
1b	**0.65**	**0.59**	**0.71**	**0.94**	**0.71**	**0.76**
1c	**0.71**	**0.95**	**0.75**	**0.72**	**0.74**	**0.79**
2a	**0.73**	**0.72**	**0.68**	**0.37**	**0.71**	**0.82**
2b	**0.05**	**0.27**	**0.38**	−0.64	**0.29**	**0.79**
3	−0.85	−0.85	−0.85	**0.69**	−0.85	**0.90**
4	**0.76**	**0.60**	**0.43**	**0.57**	**0.56**	**0.99**
5	−0.09	−0.28	−0.36	**0.97**	−0.29	**0.91**

after stimulus-offset and in Experiment 1 was 10 s post offset. Gratings with a large chromaticity difference were reportedly perceptually unstable and uncomfortable to look at. For example, a red heart on a blue or green background can cause an illusion that the heart is 'fluttering' (Wade, 1983). The most obvious explanation for the instability and discomfort is that as a result of longitudinal chromatic aberration, the accommodative system was unable to maintain a steady accommodation on the grating. Such an explanation is not, however, tenable. Haigh et al. (2013) used a laser optometer to measure accommodation to chromatic gratings identical to those used here and demonstrated no effect of the chromaticity separation on either the mean accommodative response or its fluctuation.

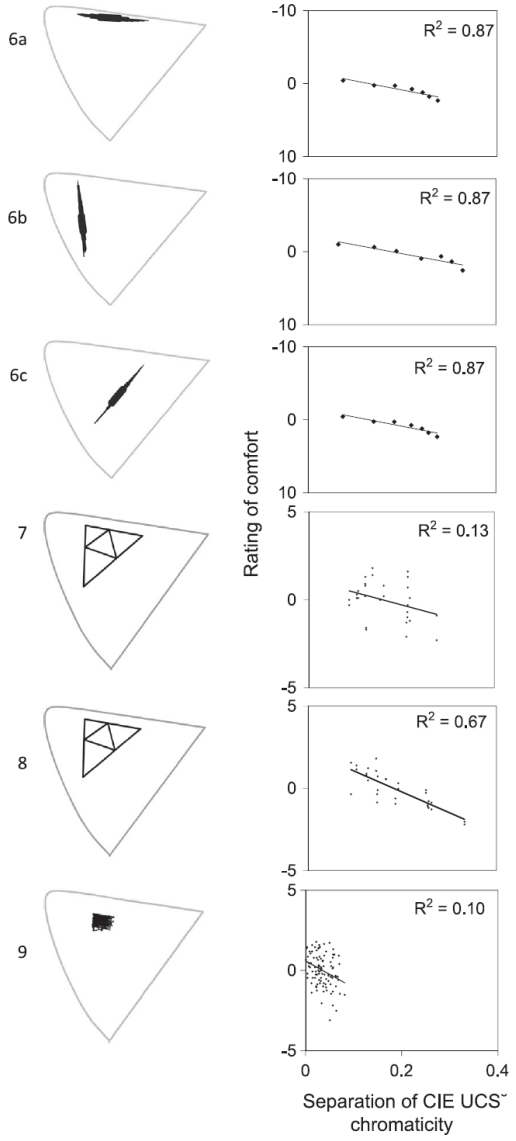


Fig. 3. Ratings of (dis)comfort from coloured gratings shown in the right hand panels as a function of the separation of the chromaticities of their bars. The ratings are from Experiments 6–9; comfort increases on the ordinates. Lines connect the chromaticities in the inset chromaticity diagrams, and where superimposed are segregated by their thickness.

The following experiments demonstrate that the discomfort is proportional to chromaticity difference regardless of hue.

4. Experiments 6–9

4.1. Methods

Forty-eight students from the University of Essex took part: six in Experiment 6, 10 in Experiment 7, 12 in Experiment 8 and 20 in Experiment 9. All were aged 18–45 (mean 20).

Participants were asked to rate the discomfort from each of a series of chromatic square-wave gratings using a ten-point scale of 1–10 in Experiment 6 and in the remaining experiments an 11-point scale ranging from −5 (very uncomfortable) to +5 (very comfortable). In Experiment 6 the gratings were circular in outline and subtended 20 deg. In the remaining experiments the gratings were square in outline and subtended 10 deg. The gratings were presented on a grey background at the centre of the LCD screen of a laptop computer (resolution 1024 × 768) from a distance of 0.6 m. Across experiments, the spatial frequency ranged from 1.5 to 3 cpd and the space-averaged luminance was constant but across experiments ranged between 9 and 30 cd m^{-2}, depending on the size of the gamut used. The gratings were displayed in a darkened room, each for 3 s. Each grating was preceded for 1 s by a central fixation cross and followed by a grey uniform screen containing a horizontal annotated scale to guide the participant's rating. Participants wore any habitual refractive correction for near vision. The chromaticities used for each grating are represented by the ends of the lines in the chromaticity diagrams in Fig. 2. The lines vary in thickness so as to segregate those on the same axis. In Experiment 6, the gratings were selected as in Experiment 1 from the edges of the screen gamut with chromaticity pairs that varied in separation but had a collective mean chromaticity midway between the vertices of the gamut. In Experiment 7 and 8, all 15 possible combinations of the chromaticities shown by the line ends in Fig. 2 were used twice. In Experiment 9 the pairs were randomly selected. The gamut was restricted by the requirement that all grating bars had the same photometric luminance.

4.2. Results

For all experiments, the ratings were internally consistent: Cronbach's alpha was 0.911 in Experiment 6, 0.871 in Experiment7, 0.730 in Experiment 8, and 0.719 in Experiment 9. The Pearson correlations between the mean rating and the separation of CIE UCS chromaticity ranged from −0.32 to −0.99 and were all significant, see Fig. 3. The average slope of the regression was −9.20. Note that this value lies within the 95% confidence limits of all the functions shown in Fig. 3.

5. Discussion

There was a consistent positive correlation between ratings of discomfort and the perceptual difference in the colour of the component bars of the grating (measured as the separation in their CIE 1976 UCS chromaticity). The random presentation of a wide range of differently coloured gratings is likely to have reduced any tendency for participants to have rated the discomfort simply on the basis of the perceived colour difference. The effect of chromaticity separation remains significant regardless of the number and colour pair of the gratings presented.

Shepherd, Hine, and Beaumont (in press) measured the effect of alternating cardinal-colour and black gratings on discomfort and visual illusions in migraineurs compared to non-migraineurs. All the colours (green, purple, red, yellow) reduced the number of illu-

sions reported by migraineurs, but had little effect on the control group. There were no obvious group colour preferences, again suggesting that discomfort is not related to hue angle, at least for the group taken together.

The results presented here suggest that perceptual colour space is a better predictor of discomfort (and oxyhaemoglobin amplitude) compared to cone-activation or colour difference channels. This supports several previous studies (Goddard et al., 2010; Parkes et al., 2009) suggesting a cortical transformation into a perceptual colour space (Brouwer & Heeger, 2009; Parkes et al., 2009). As mentioned previously, any colours that fell close to the S-cone confusion line may be less detectable than other colours, due to the differences in the contrast-sensitivity threshold for the three cone types, but this difference did not appear to affect the simple relationship between ratings of discomfort and the separation of CIE 1976 UCS chromaticity.

The luminance of the colours used varied from 9 to 30 cd m^{-2} which, though low, is typical of other studies in the literature, possibly because of the requirement for a large gamut.

The large chromaticity separation produced the largest haemodynamic response (Experiments 1–5) and the greatest discomfort (Experiments 6–9). It is therefore possible that the discomfort is homeostatic, and signifies a large metabolic demand. This would be consistent with other evidence from fMRI BOLD measurements. During the observation of achromatic patterns, Huang et al. (2011) showed that the BOLD amplitude is greatest for mid-range spatial frequencies at which the discomfort is greatest. Individuals with migraine, who are particularly susceptible to discomfort from gratings, showed a higher amplitude BOLD response, and the abnormality was greatest for mid-range spatial frequencies.

6. Conclusions

The separation in chromaticity was the only metric that was consistently associated with the amplitude of the haemodynamic response. The energy captured by the cones and the colour difference channels did not consistently covary with the amplitude of the hemodynamic response, or even the discomfort. At the cortical level colour differences may be represented neurologically in a space similar to that of the CIE 1976 UCS diagram.

Acknowledgments

We thank Roger Deeble and the late Michael Lodge for technical help. We also thank Chris Cooper and Clare Elwell for advice on near infrared spectroscopy, and the reviewers for their comments.

References

Brouwer, G. J., & Heeger, D. (2009). Decoding and reconstructing color from responses in human visual cortex. *Journal of Vision, 9*(8), 365.

Coutts, L. V., Cooper, C. E., Elwell, C. E., & Wilkins, A. J. (2012). Time course of the haemodynamic response to visual stimulation in migraine, measured using near-infrared spectroscopy. *Cephalalgia, 32*, 621–629.

Duncan, A., Meek, J. H., Clemence, M., Elwell, C. E., Fallon, P., Tyszczuk, L., et al. (1996). Measurement of cranial optical path length as a function of age using phase resolved near infrared spectroscopy. *Pediatric Research, 39*, 889–894.

Goddard, E., Mannion, D. J., McDonald, J. S., Solomon, S. G., & Clifford, C. W. G. (2010). Combination of subcortical color channels in human visual cortex. *Journal of Vision, 10*(5), 25.

Haigh, S. M., Jaschinski, W., Allen, P. M., & Wilkins, A. J. (2013). Accommodation to uncomfortable patterns. *Perception, 42*(2), 208–222.

Huang, J., Zong, X., Wilkins, A., Jenkins, B., Bozoki, A., & Cao, Y. (2011). FMRI evidence that precision ophthalmic tints reduce cortical hyperactivation in migraine. *Cephalalgia, 31*, 925–936.

Hunt, R. W. G. (1991). *Measuring colour*. Ellis Horwood Ltd.: Chichester, West Sussex.

Laeng, B., Hugdahl, K., & Specht, K. (2011). The neural correlate of colour distances revealed with competing synaesthetic and real colours. *Cortex, 47*, 320–331.

Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience, 10*, 649–669.

Livingstone, M. S., & Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience, 4*, 309–356.

MacIntosh, B. J., Klassen, L. M., & Menon, R. S. (2003). Transient hemodynamics during a breath hold challenge in a two part functional imaging study with simultaneous near-infrared spectroscopy in adult humans. *NeuroImage, 20*, 1246–1252.

MacKenzie, K. J., Hoffman, D. M., & Watt, S. J. (2010). Accommodation to multiple focal-plane-displays: Implications for improving stereoscopic displays and for accommodation control. *Journal of Vision, 10*(8), 22.

McAdam, D. L. (1981). *Color measurement*. Berlin: Springer-Verlag.

McDonald, C. T., & Burkhalter, A. (1993). Organization of long-range inhibitory connections with rat visual cortex. *Journal of Neuroscience, 13*(2), 768–781.

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. *European Journal of Neuroscience, 25*, 491–502.

O'Hare, L., & Hibbard, P. B. (2013). Visual discomfort and blur. *Journal of Vision, 13*(5), 7.

Page, E. B. (1963). Ordered hypotheses for multiple treatments: A significance test for linear ranks. *Journal of the American Statistical Association, 58*(301), 216–230.

Parkes, L. M., Marsman, J.-B. C., Oxley, D. C., Goulermas, J. Y., & Wuerger, S. M. (2009). Multivoxel fMRI analysis of color tuning in human primary visual cortex. *Journal of Vision, 9*(1), 1.

Salzmann, M. F. V., Bartels, A., Logothetis, N. K., & Schüz, A. (2012). Color blobs in cortical areas V1 and V2 of the new world monkey *Callithrix jacchus*, revealed by non-differential optical imaging. *Journal of Neuroscience, 32*(23), 7881–7894.

Shepherd, A. J., Hine, T. J., & Beaumont, H. M. (in press). Color and spatial frequency are related to visual pattern sensitivity in migraine. Headache.

Stepanyants, A., Martinez, L. M., Ferecskó, A. S., & Kisvárday, Z. F. (2009). The fractions of short- and long-range connections in the visual cortex. *PNAS, 106*(9), 3555–3560.

Strangman, G., Culver, J. P., Thompson, J. H., & Boas, D. A. (2002). A Quantitative Comparison of Simultaneous BOLD fMRI and NIRS Recordings during Functional Brain Activation. *NeuroImage, 17*, 719–731.

Tanigawa, H., Lu, H. D., & Roe, A. W. (2010). Functional organization for color and orientation in macaque V4. *Nature Neuroscience, 13*(12), 1542–1548.

Toronov, V., Webb, A., Choi, J. H., Wolf, M., Michalos, A., Gratton, E., et al. (2001). Investigation of human brain hemodynamics by simultaneous near-infrared spectroscopy and functional magnetic resonance imaging. *Medical physics, 28*, 521–527.

Ts'o, D. Y., & Gilbert, C. D. (1988). The organization of chromatic and spatial interactions in the primate striate cortex. *Journal of Neuroscience, 8*, 1712–1727.

Vautin, R. G., & Dow, B. M. (1985). Color cell groups in foveal striate cortex of the behaving macaque. *Journal of Neurophysiology, 54*, 273–292.

Wade, N. J. (1983). *Brewster and wheatstone on vision*. London: Academic Press.

Xiao, Y., Wang, Y., & Felleman, D. J. (2003). A spatially organized representation of colour in macaque cortical area V2. *Nature, 421*, 535–539.