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# Discomfort and the cortical haemodynamic response to coloured gratings

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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.

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## 1. Introduction

Colour coding in the visual cortex has been the subject of longstanding 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

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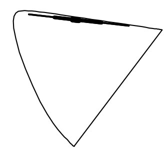
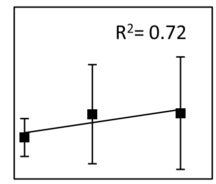
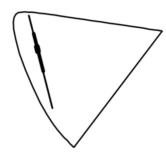
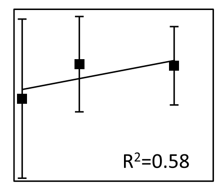
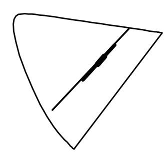
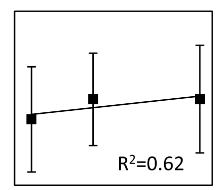
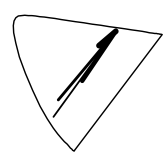
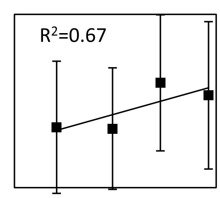
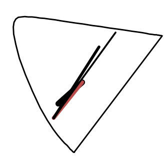
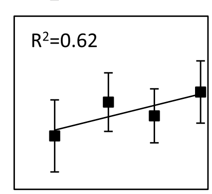
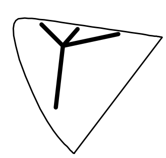
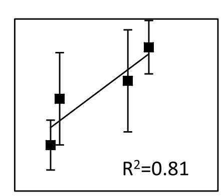
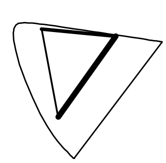
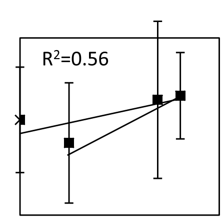
**Table 1**
The grating colours described in words and in terms of their CIE UCS 1976 chromaticity coordinates. The coordinates are shown by the ends of lines in the inset CIE UCS diagram. Where superposed, the lines vary in thickness. The amplitude of the haemodynamic response is shown as a function of the separation of the chromaticities of the grating bars, 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 gratings. Error bars show standard deviations.

| Experiment | Description | Chromaticity coordinates | | | | CIE UCS diagram | NIRS amplitude |
|---|---|---|---|---|---|---|---|
| | | first colour | | second colour | | | |
| | | u' | v' | u' | v' | | |
| 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 | | |

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