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Chromaticity separation and the alpha response

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ABSTRACT

Chromatic gratings can be uncomfortable to view and can evoke a large haemodynamic response. Both the discomfort and the amplitude of the haemodynamic response increase monotonically with the perceptual difference in the colour of the component bars of the grating, as registered by the separation in their chromaticity in the CIE 1976 UCS diagram. Individuals with photosensitive epilepsy exhibit epileptiform EEG activity in response to flickering light of alternate colours. The probability of the epileptiform response again increases monotonically with the separation of the colours in the CIE UCS diagram. We investigated whether alpha power, which is known to reflect the excitation of large populations of neurons, is similarly affected by the separation in chromaticity. Chromatic square-wave gratings with bars that differed in CIE UCS chromaticity were presented, together with a central fixation cross. In 18 non-clinical participants, alpha responses were recorded over the visual cortex (O1, Oz, O2, PO3, POz, PO4, P1, P2) and compared to responses in prefrontal cortex (F1, F2). Gratings comprised bars of two alternate colours that either had a small difference in chromaticity (mean CIE UCS separation of 0.03), a medium difference (mean separation of 0.19), or a large difference (mean separation of 0.43). The colour pairs had chromaticities that lay on the red-green, red-blue, or blue-green borders of the screen gamut. Regardless of the hue, the larger the separation in chromaticity, the greater the alpha desynchronization and the lower the alpha power ($p = 0.004$), but only in posterior electrodes ($p < 0.001$). Together this indicates that differences in colour evoke a cortical excitation that increases monotonically with the colour difference. In this respect the alpha response resembles the haemodynamic response.

1. Introduction

Discomfort from visual stimuli can be largely accounted for by the parameters of the stimulus (Penacchio and Wilkins, 2015). Uncomfortable images contain high contrast energy at mid-range spatial frequencies (Fernandez and Wilkins, 2008). One example of a high-energy image is a block of text, which comprises high contrast stripes (Wilkins and Nimmo-Smith, 1987). Achromatic mid-range spatial frequency gratings (stripes) produce a larger fMRI BOLD response compared to low or high spatial frequencies, particularly in individuals with migraine (Huang et al., 2003). Mid-range spatial frequencies are known to be epileptogenic, evoke visual illusions (Wilkins et al., 1984), and be uncomfortable to view, especially so for individuals with migraine (Marcus and Soso, 1989; Haigh et al., 2012). However, the contribution of colour to visual discomfort is often overlooked.

The majority of studies investigating the adverse effects of colour have focused on the link between chromatic flicker and seizures in patients with photosensitive epilepsy. During a television episode of Pokémon aired in 1997 in Japan, about 700 adults and children were hospitalised with seizures after the background of one of the scenes alternated between red and blue at a frequency of 12.5 Hz for 4 s. It was already known that achromatic flicker could cause seizures in patients with photosensitive epilepsy (Harding and Jeavons, 1994; Binnie, Findlay and Wilkins, 1985), but the effects of chromatic flicker were largely unknown. Many of the original studies, some preceding the Pokémon incident had identified red flicker as the most likely to induce a photoparoxysmal response (PPR) (e.g. Takahashi and Tsukahara, 1998). Parra, Lopes da Silva, Stroink and Kalitzin (2007) however, found that it was specifically the alternating red-blue flicker that produced more PPRs than other colour mixtures at low (~10 Hz) frequencies. Bhagat et al. (2009) also found that the red-blue flicker (closely followed by the red-green flicker) produced more PPRs than blue-green flicker. However, it may not be the colour per se that causes the discomfort, but the chromatic contrast in the flicker. Red-blue colours may have a larger chromaticity separation than blue-green.

To measure systematically the effect of chromatic contrast on visual discomfort, Haigh et al. (2013) obtained ratings of discomfort from

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horizontal gratings with stripes of alternate colours of similar luminance. They found that regardless of the specific colour-pair used, there was a monotonic increase in discomfort with the separation in chromaticity. Similarly, there was a monotonic increase in the amplitude of the NIRS oxyhaemoglobin response as a function of the separation in chromaticity., These relationships were most evident when using the Commission Internationale de L'éclairage (CIE) Uniform Chromaticity Scale diagram (UCS) 1976, which is a chromaticity diagram that maximises perceptual uniformity. There was no significant relationship with discomfort or haemodynamic response when colour difference was calculated according to cone activation without adjustment for perceptual colour difference (e.g. by adjustment of the S/(L+M) coordinate in MacLeod-Boynton colour space). Although the stimuli presented by Haigh et al. (2013) varied chromaticity across spatial patterns, and the studies in photosensitive epilepsy varied chromaticity in time as flicker, individuals with photosensitive epilepsy who are sensitive to flicker are also sensitive to grating patterns (Wilkins et al., 1975, 1979). Together this suggests that the separation of chromaticity may contribute both to visual discomfort, and to the photoparoxysmal activity in patients with photosensitive epilepsy.

The visual discomfort from images has been thought to be evoked as a result of excitability within the visual cortex (Bargary et al., 2015), and hence those individual with a hyper-excitable cortex are more sensitive to these stimuli (e.g. individuals with photosensitive epilepsy or migraine). The larger metabolic responses to uncomfortable images suggest a greater neural excitation. Although the metabolic response is an indirect measure of neural activity, it is associated with changes in more direct measures. The electroencephalogram (EEG) measures the electrical changes produced by large populations of neurons, and EEG responses, in particular the alpha response (8–12 Hz), have been associated with changes in metabolic response (Singh et al., 2003; Zumer et al., 2010; Brookes et al., 2005). Singh et al. (2003) was one of the first to find that areas of the cortex that showed an increase in fMRI signal, also showed event-related desynchronization in the alpha band (which is a measure of alpha suppression). Mayhew et al. (2013) found that the fluctuations in the alpha response could explain some of the variance in the BOLD response. Furthermore, visual stimuli that were presented during the trough of the alpha wave produced a larger BOLD response compared to stimuli presented during the peak of the alpha wave, suggesting that the alpha response is closely related to cortical excitability (Scheeringa et al., 2011).

In the current study, we used the same stimuli as reported by Haigh et al. (2013) to measure the alpha response, which includes stimuli that are known to be uncomfortable to view and evoke a large haemodynamic response. We recorded the EEG in response to chromatic square-wave gratings that were photometrically similar in their overall luminance and varied with respect to the separation between the chromaticities of the component bars. It was expected that the larger the chromaticity separation, the greater the alpha suppression.

2. Materials and methods

2.1. Participants

Nineteen females and three males from the University of Essex participated in the study; mean age 21.2 (range 18–54). All had a minimum of 6/6 visual acuity (Lighthouse Test for Near and Far Visual Acuity), a minimum stereo acuity of 60 sarc (Titmus test; Stereo Optical Co. In., Chicago, IL, USA), and showed no red-green colour deficiencies (Ishihara plates). This study complied with the Code of Ethics of the World Medical Association (Declaration of Helsinki), and was approved by the University of Essex Review Board. All participants gave their informed consent.

2.2. Apparatus

The stimuli were displayed on a 24″ LCD Dell screen with a backlight refresh rate of 162.5 Hz. The screen was powered by a Mac G4 Powerbook.

The electrophysiological response was measured using a NeuroScan SynAmps RT system (Compumedics USA Inc, Charlotte, NC, USA), and analysed using NeuroScan Scan 4.5 (Compumedics, Melbourne, Australia). Impedances for all electrodes were reduced to below 15 kOhm before the start of each session. All data were continuously sampled at 1000 Hz with a bandpass filter of 0.1–200 Hz and a 50 Hz notch filter. Online, EEG data were referenced to the left mastoid, and grounded at FPz. The electrode placement is shown in Fig. 1 with the labels appropriate for the 10–20 system for electrode placement. Four electrodes were placed around the eyes to record blinks and eye movement. One electrode was placed above the left eye, and another below the left eye. One electrode was placed on the outer canthus of the left eye and another was placed on the outer canthus of the right eye.

2.3. Stimuli

Gratings were displayed using SuperLab version 4.0.7b. To select the chromaticities, the three extremes of the screen gamut (red only, green only and blue only pixels) were measured using a telespectroradiometer (model PR-670®, Photo Research®, Chatsworth, CA, USA). The midpoints (29 cd/m^2) between each of the three extremes that had similar photometric luminance were calculated. Chromaticities equidistant from either side of the midpoint were then used in alternating stripes to create red-green (RG), green-blue (GB) and red-blue (RB) grating patterns. The spatial frequency of the patterns was 2cpd at a viewing distance of 1 m. Three colour pairs were created for each gamut extreme: a small separation of chromaticities in the CIE UCS 1976 diagram (mean separation of the chromaticities = 0.03), a medium separation (mean separation of the chromaticities = 0.19) and a large separation (mean separation of the chromaticities = 0.43). See Table 1 for CIE UCS co-ordinates. The gratings were circular in outline, subtended 10 deg, and were surrounded by a grey field of similar luminance ($u' = 0.192$, $v' = 0.475$, $Y = 35.3$). A central black fixation cross was shown throughout the trial (subtending 1.3 degrees of visual angle; example shown in Fig. 2. Stimuli available as tiff files in Supplementary material).

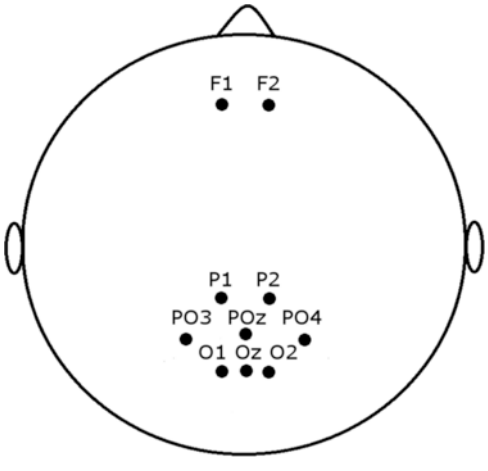

Fig. 1. Placement of electrodes used. The anterior channels (F1 and F2) were used as control channels to test for systemic effects of the stimuli, compared to the posterior channels (P1, P2, PO3, POz, PO4, O1, Oz, and O2) that would indicate local (visual) effects.

Table 1
CIE UCS 1976 u′ v′ Y co-ordinates (Y is luminance) for each colour in a pair, for the large separations in chromaticity (mean separation of the chromaticities = 0.43), medium (mean separation = 0.19), and small (mean separation = 0.03), separately for green-blue colours (GB), red-green colours (RG) and red-blue colours (RB).

Separation of chromaticity		Large		Medium		Small	
Colour pairs		1	2	1	2	1	2
GB	u′	0.165	0.067	0.127	0.086	0.106	0.101
	v′	0.181	0.571	0.337	0.496	0.421	0.440
	Y	18.58	28.96	25.89	28.19	27.92	27.47
RG	u′	0.067	0.484	0.174	0.370	0.250	0.275
	v′	0.571	0.523	0.559	0.536	0.550	0.547
	Y	30.17	30.66	31.26	32.87	39.51	36.61
RB	u′	0.165	0.484	0.294	0.426	0.354	0.383
	v′	0.181	0.523	0.308	0.455	0.374	0.406
	Y	18.31	29.07	24.28	26.78	27.66	27.51

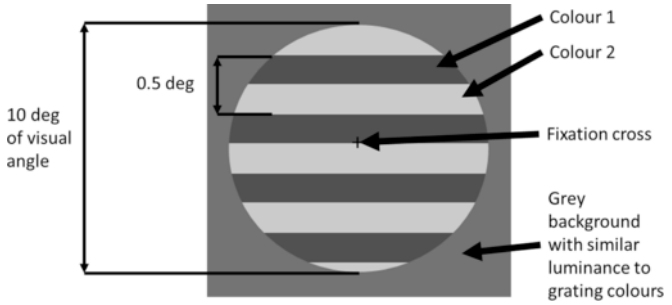

Fig. 2. An example grey-scale version of the stimuli presented. The stimuli are available as tiff files in online Supplementary material.

2.4. Procedure

Each stimulus was presented for 1 s followed by a grey screen lasting 1 s, and this pair of stimuli was presented 8 times. There were sufficient stimulus repetitions to record a reliable alpha response. The 16 s presentation was then followed by a grey screen which lasted for an interval that varied randomly between 27 and 36 s with a uniform probability distribution. The order of the stimuli was randomized and each pattern was presented twice. Each trial of 8 presentations began with a grey screen. The participants viewed the stimuli binocularly in a darkened room and were asked to fixate on a cross displayed at the centre of the screen throughout the trial.

2.5. Data analysis

For the electrophysiological response, all channels were re-referenced to the average of the two mastoids. The sections of the data that contained blink and movement artefact were removed after inspection of the record. The electrodes placed above and below the left eye were used as a guide to delete sections of the recording that contained a blink. Sections of the recording when there was a sudden increase in the noise in the signal across all electrodes due to movement artefact were removed. As a result, all the epochs from four participants were excluded from analysis. A further off-line automated artefact rejection transform was also carried out, excluding data above 75 μV or below −75 μV. This led to the data from an additional participant being excluded from analysis, resulting in eighteen participants' data being analysed.

To measure the event-related desynchronization in the alpha band, the recording was divided into epochs starting 600 ms before stimulus onset, and ending 1300 ms after stimulus onset. The signal from the remaining epochs were separated into the alpha (8–12 Hz) band using complex demodulation and concurrent filtering (zero-phase shift, 24 dB roll-off, envelope computed). The epochs were trimmed by 300 ms from each end to remove warm-up artifacts. The signal 300 ms before stimulus onset to the point of stimulus onset was used as the reference, using an adapted method from Pfurtscheller (1977) and Pfurtscheller and da Silva (1999) where % change in ERD = (reference period-stimulus presentation/reference period)* − 100, resulting in event-related desynchronization producing negative scores, containing both phase-locked and non-phase-locked activity. The effect of the stimulus was calculated according to the percent change in the event- related band power at each frequency range. The reference for calculating the change in event-related band power was from 300 ms before stimulus onset to stimulus onset.

The effect of chromaticity separation was assessed in a repeated-measures analysis of variance (ANOVA) with chromaticity separation (small, mid, and large), electrode position (frontal, parietal, parietal-occipital, and occipital electrodes), and laterality (1, z, and 2) as within-subjects factors. A separate repeated-measures ANOVA was used to assess the effect of colour-pair (RG, RB, and GB), electrode position, and laterality as within-subjects factors. All statistics were run in R, and only significant main effects and interactions are reported.

3. Results

There was an increase in alpha suppression with chromaticity separation ($F(2,495) = 5.60$, $p = 0.004$), and a main effect of electrode position ($F(3,495) = 7.58$, $p < 0.001$) because anterior (F1 and F2) electrodes had less alpha desynchronization during stimulus presentation compared to posterior (visual) electrodes (O1, Oz, O2, PO3, POz, PO4, P1, and P2). However, there was only a small and non-significant interaction between electrode position and chromaticity separation ($F(6,495) = 1.96$, $p = 0.070$; Fig. 3).

For colour pairing, there was a significant effect of colour pair in the posterior electrodes ($F(2,495) = 10.10$, $p < 0.001$) due to the greater alpha suppression from the RG grating than the RB ($p < 0.001$) and the GB gratings ($p = 0.013$). There was also a significant effect of electrode position ($F(2,495) = 9.60$, $p < 0.001$), due to the greater desynchronization from posterior electrodes than anterior ($p < 0.001$). There was no significant interaction between electrode position and colour pair ($F(2,6) = 0.87$, $p = 0.519$).

4. Conclusions

The greater the separation in chromaticity between the bars of the grating stimuli the greater the alpha suppression. The suppression was localised in the visual cortex and was not a systemic effect that propagated across the cortex, consistent with increased visual cortical excitation. This finding is also consistent with the previous reports of the effect of chromaticity difference on the amplitude of the haemodynamic responses to gratings and the fact that this response is over posterior

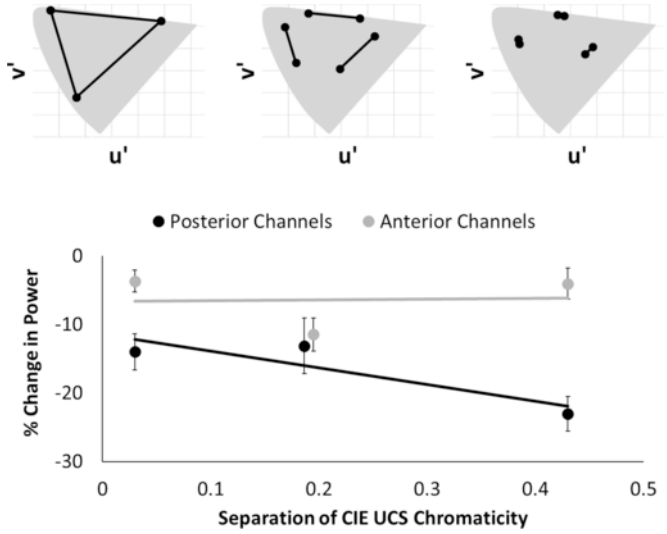

Fig. 3. Percent change in alpha power as a function of chromaticity separation (slightly offset for clarity) for posterior electrodes (O1, Oz, O2, PO3, POz, PO4, P1 and P2) and anterior electrodes (F1 and F2), with linear regression lines added. Error bars represent one standard error.

regions (Haigh et al., 2013). The excitation exemplified in both the alpha suppression and the haemodynamic response could be responsible for the reports of discomfort, which is similarly affected by the difference in chromaticity.

Overall, the RG gratings produced greater alpha suppression than the RB and GB gratings. This was unexpected, because there was no overall bias in ratings of discomfort, nor in the haemodynamic response as measured using NIRS (Haigh et al., 2013). One limitation of this study is that discomfort data were collected in previous studies but not here, and so it is difficult to tell if there was a bias to the RG grating in these individuals in their subjective ratings of discomfort. While the colour pairs in each grating were photometrically similar in their luminance (Table 1), the luminance of the RG gratings was higher than the luminance of the RB and GB gratings, which may explain the greater alpha desynchronization to RG gratings.

Table 2
The CIE UCS 1976 u′ v′ co-ordinates for the individual colours used in the flicker paradigm by Parra et al. (2007), estimated from their Fig. 1.

	Blue	Green	Red	Yellow
u′	0.11	0.05	0.60	0.32
v′	0.24	0.57	0.51	0.54

Table 3
An approximate summed Z-scores from Fig. 3 of Parra et al. (2007), number of patients that exhibit sensitivity, and number of photoparoxysmal responses (PPRs) to each of the coloured flicker pairs, all shown as a function of separation in CIE UCS 1976 chromaticity for each of the flickering stimuli.

	Chromaticity separation	Z-scores	Patients (n)	PPRs (n)
Blue-Red	0.56	3.7	25	50
Red-Green	0.55	3	20	42
Green-Blue	0.33	0.7	7	7
Blue-Yellow	0.37	2.6	17	37

Previous studies of aversive effects have focused on the contribution of specific colour pairs alternating in time as a flickering stimulus. The gratings used in the current study vary in chromaticity across space. However, chromaticity separation can explain the photoparoxysmal activity evoked by chromatic flicker. Parra et al. (2007) found that red-blue flicker was particularly epileptogenic. However, when the colours in the flicker were transformed to CIE UCS 1976 colour space (Table 2), the chromaticity separation differed. When the chromaticity separation of the flicker is plotted against the z-score of sensitivity, or the number of patients that exhibited the sensitivity, or the number of PPRs, the relationship is monotonic in each instance (Table 3; Fig. 4). The effect of chromaticity separation in flicker may differ from the effect in gratings, but the difference in chromaticity accounts for 70.4%, 75.0% and 66.6% of the variance in each of the relationships show in Fig. 4.

Here we demonstrate that alpha desynchronization can be driven by changes in chromaticity separation. It is interesting to note that in the current study, the bars of each pattern were photometrically similar in luminance, and so the change in alpha power was due to changes in chrominance. Subjective luminance can differ slightly from photometric luminance, which could introduce some variability in alpha responses between individuals, but these effects are likely to be small. Previously, studies had found more reliable responses to achromatic than chromatic contrast (Lennie et al., 1990; Ts'o and Gilbert, 1988), with inconsistent findings as regarding colour contrast (Mullen et al., 2007). In the current study, we measured chromaticity separation in the CIE UCS 1976 diagram in which the colours are mapped so that they are perceptually approximately equidistant. Other studies that

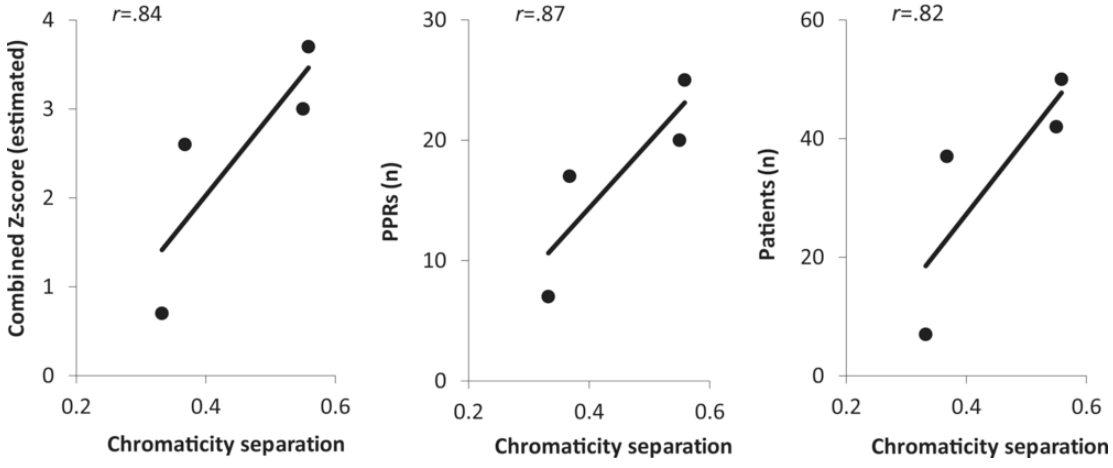

Fig. 4. Chromaticity separation (in CIE UCS 1976 colour space) in flicker as a function of the estimated combined z-score (left), the number of patients who exhibited sensitivity (centre), and the number of photoparoxysmal responses (PPRs; right). Linear regression lines added. Pearson correlations shown.

found no consistent neural responses to chromatic contrast measured colours in terms of cone activation (Mullen et al., 2007), which may explain some of the inconsistency.

Greater cortical excitation (as indicated by greater alpha suppression) in response to stimuli with large chromaticity differences provides a unifying theory as to why certain colour pairs (whether that be in flicker or in grating patterns) evoke greater visual discomfort, and increase the probability of evoking photoparoxysmal activity in individuals with photosensitive epilepsy. A possible drawback of using the CIE UCS 1976 diagram, is that there is no obvious physiological or neurological origin for the topographical organisation. Measuring chromatic contrast as a function of cone activation has a clear physiological basis. However, the DIN colour map, which like the CIE UCS diagram is organised by perceptual similarity, was found to be represented in the surface topography of macaque V2 measured using optical methods (Xiao et al., 2003), suggesting that there is a neurological basis for the UCS map. How and why colour organisation transforms from the cones through to V2 is unknown, but may have to do with colour constancy (Conway et al., 2010).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuropsychologia.2017.11.020.

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