Cortical summation and attentional modulation of combined chromatic and luminance signals

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Abstract

Cortical networks that process colour and luminance signals are often studied separately, although colour appearance depends on both colour and luminance. In fact, objects in everyday life are very rarely defined by only colour or only luminance, necessitating an investigation into combined processing of these signals. We used steady-state visual evoked potentials (SSVEPs) to investigate (1) cortical summation of luminance and chromatic contrast and (2) attentional modulation of neural activity driven by competing stimuli that differ in chromoluminant content. Our stimuli combined fixed amounts of chromatic contrast from either of the two cone-opponent mechanisms (bluish and yellowish; reddish and greenish) with two different levels of positive luminance contrast. Our experiments found evidence of non-linear processing of combined colour and luminance signals, which most likely originates in V1-V3 neurons tuned to both colour and luminance. Differences between luminance contrast of stimuli were found to be a key determinant for the size of feature-based voluntary attentional effects in SSVEPs, with colours of lower contrast than the colour they were presented with receiving the highest level of attentional modulation. Our results indicate that colour and luminance contrast are processed interdependently, both in terms of perception and in terms of attentional selection, with a potential candidate mediating their link being stimulus appearance, which depends on both chromaticity and luminance.

Keywords: colour, luminance, attention, contrast, bottom-up, top-down, SSVEPs, cone-opponent mechanisms

1. Introduction

Originating at the lower, subcortical level of representation, two cone-opponent mechanisms and one cone-additive mechanism compute information on colour and luminance in the environment, respectively (Derrington et al., 1984; for a relatively recent review, see Stockman and Brainard, 2010). At this level, colour is derived from differences in long and mid-wavelength cones (L-M; reddish vs. greenish), on the one hand, and short-wavelength cones and a combination of long and mid-wavelength cones (S-(L+M); bluish vs. yellowish), on the other, with neurons being broadly tuned around these orthogonal, cardinal axes. Meanwhile, luminance is computed by summing the signals from long and mid-wavelength cones (L+M), and, in special circumstances, also short-wavelength cones (Ripamonti et al., 2009). Low-level colour spaces such as Derrington Krauskopf and Lennie (DKL) have luminance (L+M) as a basic dimension, with the other two basic dimensions being chromatic (L-M) and S-(L+M). Perceptual colour spaces such as CIELAB, CIELUV or the Munsell colour system have different dimensions, which reflect perceptual attributes that are derived from these low-level signals. Processing of luminance contrast leads to the percepts of brightness (perceived luminance) and lightness (perceived reflectance; for a review see Kingdom, 2014), with lightness being a basic dimension of the aforementioned perceptual colour spaces. Colour content leads to (1) the dimension of hue and (2) dimensions such as chroma or colourfulness, with colourfulness being to chroma as brightness is to lightness. As the amount of colour content increases, so do colourfulness and chroma. Saturation is colourfulness of an area judged in proportion to its brightness, and thus incorporates both chromatic and luminance information (Fairchild, 2004; Schiller et al., in press).

Attention is very efficient when selecting on the basis of colour (Andersen et al., 2008; Andersen et al., 2015, Found and Muller, 1996, AnlloVento and Hillyard, 1996). However, in many experiments on attention, stimuli are not isoluminant, differing against their background

both in terms of colour and luminance (e.g., Lindsey et al., 2010; Stormer and Alvarez, 2014; Tollner et al., 2011). The underlying assumption in many of these studies is that, as long as different colours are equated to each other in terms of luminance content, often through equating lightness in a perceptual colour space, any attentional effects will reflect only the selection of colour and will not depend on the amount of luminance contrast in the stimulus. However, colour and luminance are not processed independently in the cortex (for a review of electrophysiological evidence in macaques, see Shapley and Hawken, 2011; for recent human electrophysiology studies, see Nunez et al., 2017, 2018; Xing et al., 2015). Many neurons in early visual areas respond preferentially both to a certain colour direction and to a certain level of luminance contrast (e.g., Gegenfurtner et al., 1997; Kiper et al., 1997; Li et al., 2015; for reviews, see Gegenfurtner, 2003; Solomon and Lennie, 2007). With luminance and colour conjoined in natural scenes under daylight viewing conditions, and with dedicated early resources for the joint processing of such signals, e.g. the double-opponent neurons that are sensitive to L-M contrast and whose involvement has been shown to affect perceived saturation (Nunez et al., 2018), it is essential to find out how attention operates at the behavioural and neural level when luminance and chromatic contrasts are combined in the stimulus.

In order to determine both the behavioural outcomes and the underlying neural mechanisms through which perception and selection of colour-luminance combinations operate, we conducted a steady-state visual evoked potential (SSVEP) study using an established feature-based attention paradigm that requires sustained monitoring of spatially-overlaid random dot kinematograms (RDKs) in order to detect brief coherent motion transients (e.g., Müller et al., 2006). The coherent motion task allowed us to define task-relevant events that are independent of the colour and luminance of stimuli, thus avoiding additional changes in these stimulus dimensions of interest. Further advantage of the aforementioned feature-based attention paradigm is that it allows for concurrent electroencephalographic measures of

attentional allocation to individual stimuli in a multi-stimulus display, as each of the stimuli can be "frequency-tagged" by being flickered at a different frequency and thus driving its own SSVEP response (for reviews, see Andersen et al., 2011; Norcia et al., 2015). SSVEPs are oscillatory responses of the visual cortex that have the same frequency as the driving stimulus. SSVEP amplitude is increased with both spatial and feature-based attention, while spatial attention advances the phase for luminance-defined stimuli, but not for isoluminant stimuli (Di Russo et al., 2001). SSVEP has a clear advantage for attention research over other standard methods (e.g. event-related potentials, functional magnetic resonance imaging, behavioural measures alone etc.) which cannot as easily separately assess the neural processing of multiple spatially overlapping stimuli. The sources of attentional modulations observed with feature-based SSVEP paradigms have been consistently localised to early visual areas, V1-V3 (Andersen et al., 2008; Müller et al., 2006). Thus, they have the potential to capture the output of neurons situated in those areas and provide information on whether any asymmetries exist in the early cortical summation of colour and luminance signals. Asymmetric summation of chromatic L-M signals and luminance signals was previously reported by Rudvin and Valberg (Rudvin, 2005; Rudvin and Valberg, 2005), but currently there is no data for the S-(L+M) mechanism. Our study has the potential to identify if basic differences in cortical summation extend to the level of attentional modulation, where top-down influences are implemented. If this was true, we should observe the same asymmetries in perception and attentional selection between different colours. Alternatively, top-down influences may be applied consistently to the bottom-up signals, irrespective of the cone-opponent mechanisms involved.

We investigated (1) in which way cone-opponent, chromatic and cone-additive, luminance signals are summed neurally and (2) in which way voluntary, top-down attentional selection of such colour-luminance combinations is affected by the type of cone-opponent signal that is involved and the amount of luminance contrast in the stimulus. We were

especially interested in examining if asymmetries would emerge between the two chromatic mechanisms, as well as between their respective poles (i.e. reddish vs. greenish for L-M and bluish vs. yellowish for S-(L+M)). To make our findings more directly comparable to previous work which eschewed individual differences to aim at general, cross-sample effects (e.g., Lindsey et al., 2010) we combined a lower and a higher level of fixed, relatively large positive luminance contrast with a fixed, relatively large amount of chromatic contrast, without tailoring the salience of the stimuli to individual participants.

Asymmetries in summation with luminance contrast between the two mechanisms, as well as between the two poles of the S-(L+M) mechanism (bluish and yellowish), could be expected based on previous research. Recent research into the properties of the middle layers of the koniocellular pathway, which receive S-cone inputs and thus form the geniculate substrate for the S-(L+M) mechanism, suggest that bluish and yellowish are likely to be processed differently (for a review, see Dacey et al., 2014). Faster visual search in humans and larger local field potentials in macaques are observed for yellowish as opposed to bluish hues at nominally equivalent levels of chromatic contrast (Wool et al., 2015). Bluish is perceived as less saturated than yellowish at equivalent chromatic contrasts (Schiller et al., in press; Switkes, 2008). Finally, attending to bluish does not lead to attentional enhancement of SSVEPs in the early cortical areas, but does lead to an enhancement in later area V4 (Wang and Wade, 2011). Thus, one might expect that bluish would sum less effectively with luminance signals and might represent a less effective target for voluntary attentional selection. In our first experiment, we tested summation between chromatic and luminance signals using single-colour RDKs, hypothesising that the aforementioned asymmetries would be revealed in the S-(L+M) channel. In our second experiment, we examined behavioural and neural outcomes of attentional selection of RDKs defined by colour-luminance combinations studied in the first

experiment. We predicted that bluish stimuli would elicit poorer performance and would also be subject to a lower level of early attentional modulation as evidenced by the SSVEPs.

2. Materials and methods

2.1 Participants

The sample for experiment 1 (summation) consisted of 11 participants, 5 of which participated in both the S-(L+M) and the L-M sessions, whilst the remaining 6 participated only in one of the two sessions (4 female, 1 left-handed, age range between 22 and 36, average of 25). For experiment 2 (feature-based attention), we tested 11 participants, but two participants were excluded from the sample: one was unable to achieve performance above 28% hit rate despite repeated practice blocks, while the other participant's SSVEP data was overly noisy. The final sample thus consisted of 9 participants, which participated in both the S-(L+M) and L-M sessions (5 female, 1 left-handed, age range between 21 and 34, average of 24). All subjects reported normal colour vision, which was verified with the City University Colour Vision Test (Fletcher, 1975), and normal or corrected-to-normal visual acuity. All participants gave informed consent prior to the experiment. The experiments were approved by the ethics committee of the School of Psychology at the University of Aberdeen and were in accordance with the Declaration of Helsinki.

2.2 Stimuli

Stimuli consisted of Random Dot Kinematograms (RDKs) displayed on a 21-inch calibrated Viewsonic P227f CRT monitor with a refresh rate of 120 Hz, set to a resolution of 640 x 480 pixels. The monitor was controlled using a Visage system (Cambridge Research Systems, Kent, UK) and was calibrated with a ColorCal II (Cambridge Research Systems, Kent, UK). The colour look-up tables were created based on measurements taken with a SpectroCal (Cambridge Research Systems, Kent, UK) and Stockman and Sharpe (Stockman and Sharpe,

2000; Stockman et al., 1999) cone fundamentals. Stimulus presentation and response collection were done using the CRS toolbox for Matlab (Mathworks, Nantucket, US). The DKL (Derrington et al., 1984) colour space was used to define the chromoluminant properties of the stimuli (Westland et al., 2012). This is a physiological colour space, representing mechanisms at the level of the lateral geniculate nucleus. Figure 1 (left hand side) shows a representation of the DKL isoluminant plane, indicating the two orthogonal chromatic (L-M and S-(L+M)) mechanisms.

Experiment 1 was conducted in two sessions (S-(L+M) and L-M), with the order counterbalanced in a subgroup of participants that took part in both sessions. Experiment 2 was also conducted in two recording sessions, whose order was counterbalanced across participants. In one session, the chromatic content of the RDKs was defined along the S-(L+M) axis of the DKL space, with approx. ±1.6 2S-(L+M) contrast. In the other session, the chromatic content of the RDKs was defined along the L-M axis of the DKL space, with approx. ±0.16 L-M contrast. We chose these relatively high contrast values in order to obtain highly salient stimuli that nevertheless still enabled combinations with non-negligible amounts of luminance contrast to be achieved within our monitor's gamut. Mechanism contrasts were calculated from Weber cone contrasts. The background was set to neutral grey (CIE 1931 coordinates x=0.30, y=0.32, Y=44.4 cd/m^2). Two luminance levels were used in the experiments: ~76 cd/m^2 or ~61 cd/m^2, thus both brighter than the background. This gave them the following Weber luminance contrasts: ~0.71 for higher and ~0.37 for the lower luminance contrast RDK. These are relatively high amounts of luminance contrast, lying well above the level that is normally needed to saturate the visual evoked potential (above 10-30% contrast, depending on spatial frequency; Strasburger et al., 1986; Strasburger et al., 1988). The two levels of luminance contrast were thus meant to elicit equivalent SSVEP amplitudes. Hence, any differences in SSVEP amplitudes elicited by combinations of identical colour contrast with (1) a higher or

(2) a lower level of luminance contrast would have to be caused by non-linear summation of colour and luminance contrast. There are two reasons why we used stimuli which represented positive luminance polarity: 1) such desaturated stimuli were previously used by Lindsey et al. (2010) so this choice would facilitate comparisons with their findings; 2) Rudvin, Valberg and Kilavik (2000) reported that evoked potential responses to negative luminance polarity tended to be less distinctive than for the positive polarity, and more variable between subjects (Valberg and Rudvin, 1997). Measurements of all the stimuli by a spectroradiometer (SpectroCAL, CRS, UK) are given in Table 1 in CIE 1931 colour space coordinates and in corresponding CIE Lch space coordinates, along with their contrasts. CIE Lch coordinates are presented to give the reader an idea about the perceptual attributes of the stimuli: lightness (L), chroma (c) and hue angle (h). The CIE Lch space is another way of representing the CIE Lab space, and they share one common attribute (L, or lightness, which is equivalent to relative brightness), whilst the colour coordinates of CIE Lab are replaced by chroma (equivalent to relative colourfulness) and hue, thus defining two important perceptual qualities of colour (Westland et al., 2012). Saturation is computed as a ratio of chroma to lightness, C/L, and also expressed in Table 1.

Insert Table 1 about here

Figure 1 represents all the conditions used in experiment 1 (summation). In this experiment, there was a single RDK which flickered at 10 Hz, thereby driving an SSVEP at the same frequency. Participants monitored the RDK to detect brief intervals of 50% coherent motion (0-4 per trial) interleaved in the otherwise random motion of the dots. All the

combinations of chromatic and luminance signals for experiment 2 (attention) are represented in Figure 2. In this experiment, the stimulus contained two RDKs which flickered at different rates: 10 Hz (6 frames on and off) and 12 Hz (5 frames on and off). This way each of the colours elicited a separate SSVEP wave of corresponding frequency, which allowed analysing EEG signals stemming from each of the colours separately. As in experiment 1, the task was to detect brief intervals of 50% coherent motion, but this time these events could occur either in the attended or in the unattended dots, imposing selective attention demands.

Insert Figure 1 about here

Insert Figure 2 about here

2.3 Procedure

Participants were seated in a comfortable chair in an electrically shielded booth, at 80 cm from the CRT screen which was the only source of illumination. In a preliminary session, each participant performed several practice blocks of the experiment, until they acquainted themselves with the task and their hit rates were above 60%. During the practice block, participants received auditory feedback to assist them with learning the task. Auditory feedback was not given during the experiments themselves.

Each trial started with a white fixation cross (size: 0.32 degrees of visual angle) presented in the centre of the screen for approximately 3 seconds. In experiment 2, afterwards a *cue* was presented for 600 msec. The cue consisted of a static pattern of a single-colour set of 120 dots: yellowish, bluish, reddish or greenish. Participants were instructed to attend the cued colour in the subsequent movement interval. After the cue, a neutral grey screen with a

fixation cross was presented again for 750-1000 msec, after which one RDK (experiment 1) or two overlapping RDKs (experiment 2) were presented for 6500 msec (see Figure 3). The RDKs were 9.60 degrees of visual angle in diameter and consisted of 120 square-shaped dots whose sides were 0.28 degrees of visual angle. The RDKs differed in colour and luminance contrast, as explained previously (in one session, bluish and yellowish; in the other session, reddish and greenish). In Experiment 2 (attention), the two colours were displayed either both at a higher luminance level (~76 cd/m^2), both at a lower luminance level (~61 cd/m^2), or one of them at the higher and the second one at the lower luminance level (see Figure 2). All dots within the RDKs moved at a speed of 0.05 degrees of visual angle per frame randomly and independently of each other, except for sporadic brief coherent motion intervals. At these intervals of coherent motion, 50% of the dots from one of the RDKs moved in a synchronised way either vertically or horizontally (see Figure 3). Such coherent motion occurred between 0 and 4 times in each trial and lasted 400 ms. The 50% of the dots that moved in unison were chosen randomly for each of the frames that constituted the 400 ms coherent motion period. In Experiment 2 (attention), participants were instructed to respond with a button press each time they detected such coherent motion within the cued RDK (target), and ignore coherent motion within the uncued RDK (distractor). In experiment 1 there was only the target RDK so the task required simple coherent motion detection. The onset of targets and distractors happened no earlier than 500 ms after the onset of the RDK. There was a time window of 250 to 900 ms after each target for the participant to respond. Subsequent targets and distractors onsets were separated by at least 700 ms. For both experiment 1 and experiment 2, there was a total of 8 blocks of trials in each of the two sessions, each consisting of 48 trials. Experiment 1 contained 80 coherent motion targets per experimental condition (thus 640 events in total), whilst Experiment 2 contained 320 coherent motion targets and 320 distractors (40 of each per experimental condition). Events were distributed randomly between all 8 blocks.

Insert Figure 3 about here

2.4 EEG recording and analysis

EEG was recorded at a sampling rate of 256 Hz using 64 Ag/AgCl electrodes mounted in an elastic cap with a BioSemi ActiveTwo amplifier system (BioSemi, Amsterdam, the Netherlands). Horizontal eye movements were monitored with a bipolar outer canthus montage, while vertical eye movements and blinks were monitored with a bipolar montage positioned below and above the right eye.

EEG data were processed using the EEGLab toolbox (Delorme and Makeig, 2004) in combination with custom Matlab scripts (The Mathworks, Natick, Massachusetts). The first 500 ms after the onset of the RDK were discarded to allow the SSVEP to build up and to exclude the transient VEP to stimulus onset. From the remaining 6000 ms of each trial, 6 epochs of 1000 ms were extracted. All epochs with target or distractor events or manual responses within the epoch were excluded from the SSVEP analysis. Epochs with eye movements or blinks were rejected from further analysis, using a criterion of ±25 μV for horizontal eye movements, and all remaining trials with artifacts were rejected by means of an automated procedure, which detected contaminated trials and noisy channels that needed interpolation (either in the entire EEG recording or on any single trials) by calculating statistical parameters of the data and using a Z-score of ±3 for that parameter as metric that defined contaminated data (FASTER; Nolan et al., 2010). Data were detrended and re-referenced to the average of all electrodes after artifact correction. Visual inspection was then used to confirm the accuracy of the artifact correction procedure. On average, 155 epochs per condition (88%; 176 total

trials) remained after the rejection in Experiment 1, and 141 epochs per condition (76%; 186 total trials) remained after rejection in Experiment 2. Complex valued SSVEP amplitudes z (amplitude vectors) were obtained from the Fourier coefficients at the respective flicker frequencies. Absolute SSVEP amplitudes are the Euclidean length of the complex amplitudes z (Matlab function 'abs'):

$$|z| = \sqrt{Re(z)^2 + Im(z)^2} \qquad (1)$$

The latency of SSVEPs was obtained by first computing the phase φ (in radians) of the complex amplitudes z (Matlab function 'angle')

$$\varphi = atan2(Im(z), Re(z)) \quad (2)$$

and then converting them to latencies l using the frequency f of the SSVEP:

$$l = -\frac{\varphi}{2\pi f} \qquad (3)$$

2.5 Heterochromatic Flicker Photometry

Individual differences in the luminosity function (Vλ) can result in a small luminance signal being present within the nominally isoluminant stimulus (Wyszecki and Stiles, 2000). Even though most of our stimuli also contain relatively large amounts of luminance contrast, these individual differences could potentially interact with the experimental results. This could particularly be the case for L-M colours, since Vλ can be related to the function of L and M cones (e.g., Brainard et al., 2000; Dobkins et al., 2000) while the contribution from S-cones is relatively small and observed only under special circumstances (Lee and Stromeyer III, 1989). To check if this potential confound significantly impacts on SSVEPs, all participants in Experiment 1 (summation) were asked to complete a heterochromatic flicker photometry test (HCFP) which measured their observer isoluminance levels for colours from the L-M axis (reddish and greenish). In the HCFP test, participants were shown a static frame of 120 dots which flickered between reddish and greenish at a rate of 20 Hz. The colours were set to

chromatic contrast levels used in the experiments (see Table 1). By pressing left and right buttons on the response box, participants could increase or decrease the relative luminances of the colours. This flicker rate is too fast for the sluggish chromatic system to detect; however, it can be detected by the fast luminance system. Participants were asked to press the left and right button until they found a point at which the stimulus flicker was least visible. The HCFP results were then included in the ANOVA model as a co-variate for the SSVEP amplitude and latency differences for the L-M colours to check if individual differences in luminous efficiency had any contribution to main effects and interactions.

2.6. Statistical data analysis

In experiment 1 (summation), we tested whether the SSVEP responses (both in terms of phases and amplitudes, i.e. complex amplitudes) in combined conditions can be predicted using the data obtained in single contrast conditions. If SSVEPs elicited in combined conditions were found to be equal to the sum of the SSVEPs elicited in the corresponding single contrast conditions (i.e. luminance and chromatic contrast separately), then this would imply that the different contrast dimensions are either cortically combined in an additive manner or that additive superimposition of the electric fields generated by independent processing of the contrast dimensions produces the recorded signal. This was assessed by means of T^2-circular tests (Victor and Mast, 1991) in which the combined stimulus response (e.g., reddish with a higher level of luminance contrast) was subtracted from the sum of the isolated responses to its constituents (reddish in isolation and higher level of luminance contrast in isolation) and tested against zero. We also calculated differences in amplitude and latency between observed responses to combined colour/luminance stimuli and responses predicted from activity elicited by individual colour and luminance stimuli. We subjected these to 2x2 repeated measures ANOVA separately for the S-(L+M) and the L-M mechanism, with factors *unipolar colour*

mechanism (bluish or yellowish; reddish or greenish) and *luminance contrast* (lower or higher level). Subsequently, HCFP results were entered as a covariate into the ANOVAs for the L-M mechanism to see if they influenced any of the obtained effects. Finally, hit rates and reaction times were analysed using 2x3 repeated measures ANOVA, with factors *unipolar colour mechanism* (bluish or yellowish; reddish or greenish) and *luminance contrast* (isoluminant, lower, or higher level). The purpose of this analysis was to reveal any possible asymmetries between increments and decrements in the L-M or the S-(L+M) mechanisms. Statistical interactions were followed up using paired t-tests with Bonferroni correction for main effects and Tukey's HSD at $p<.05$ for interactions.

In experiment 2 (attention), for d's and reaction times (RT), we performed 2x2x2 repeated measures ANOVAs separately for S-(L+M) and L-M directions, with the following factors: *attended colour* (reddish/greenish or bluish/yellowish), *luminance contrast of target* (lower/higher) and *luminance contrast of distractor* (lower/higher). Further, d's and reaction times (RTs) were analysed using correlational models to identify if differences between targets and distractors in (1) luminance contrast or (2) colour saturation were better predictors of task performance, as addition of luminance contrast leads to desaturation. We performed correlations of average d's and RTs computed from our experimental conditions with differences between the target and distractor colours in terms of luminance contrast or saturation.

To assess attentional modulation of SSVEPs, we considered SSVEP amplitudes and phases (latencies) separately. The Attentional modulation indices (AMIs; Luck et al., 1997) for each stimulus were calculated from the SSVEP amplitude (equation 1) when it was attended (A) and unattended (U) as follows:

$$\mathrm{AMI} = \frac{\mathrm{A}-\mathrm{U}}{\mathrm{A}+\mathrm{U}} \qquad (4)$$

We also computed differences in latency between attended and unattended stimuli. Phases in radians for attended φ_A and unattended φ_U stimuli were computed as per equation (2) and used to compute the latencies of attended and unattended stimuli (l_A and l_U) using the respective frequencies f of the stimuli (10/12 Hz). The attentional latency modulation δ_l in seconds is then simply:

$$\delta_l = l_A - l_U \qquad (5)$$

Similarly to the behavioural data, AMIs and attentional latency modulation were assessed with a repeated measures ANOVA and correlational models to identify if differences in luminance contrast or saturation were better predictors of the magnitude of attentional effects. However, the analysis of the SSVEP data follows a slightly different logic than for the behavioural data and accordingly, the ANOVA factors are labelled differently. Whereas the behavioural analysis focusses on responses to brief coherent motion targets (and distractors), the SSVEP data examines the differences in the response elicited from a continuously presented stimulus when it is attended to when it is unattended. Correspondingly, we performed a 2x2x2 repeated measures ANOVAs with the factors *colour* (reddish/greenish or bluish/yellowish), *colour's luminance contrast* (lower/higher) and *competitor's luminance contrast* (lower/higher) for AMIs and attentional latency modulation, separately. 'Competitor' here refers to the luminance of the concurrently presented superimposed stimulus of different colour.

3. Results

3.1. Experiment 1: Summation

The purpose of the experiment is to capture behavioural and neural outcomes of combining colour signals from different subcortical mechanisms with luminance signals without manipulating selective attention. We analyse hit rates, reaction times and SSVEPs.

3.1.1. Behavioural results

Behavioural data (hit rates and RTs) are depicted in Figure 4. Data were analysed using a 2x3 repeated measures ANOVA, with factors *unipolar colour mechanism* (bluish or yellowish) and *luminance contrast* (isoluminant, lower, or higher level). For the S-(L+M) mechanism, there was a trend towards different hit rates for different luminance contrasts ($F(2, 14) = 3.49$, $p = .059$), and a trend for lower hit-rates for bluish than for yellowish ($F(1, 7) = 4.01$, $p = .085$) coherent motion targets. There was no interaction ($F(1.08, 7.55) = 2.73$, $p = .14$). Reaction times for bluish targets were significantly slower ($F(1, 7) = 8.40$, $p = .023$, $\eta_p^2 = .55$), and further depended on luminance contrast ($F(1.02, 7.17) = 51.44$, $p < .001$, $\eta_p^2 = .88$), with lower RTs for isoluminant stimuli ($p < .001$ and $p = .001$) and no differences between stimuli that contained luminance ($p = .86$). These effects were further qualified by an interaction ($F(1.04, 7.30) = 7.02$, $p = .031$, $\eta_p^2 = .50$), with post-hoc Tukey's HSD test (using the corrected degrees of freedom to obtain the Q value) revealing that whilst isoluminant bluish was slower than all the conditions that contained luminance, this was not the case for isoluminant yellowish. The two isoluminant colours themselves did not significantly differ.

For the L-M mechanism, hit rates were comparable across the analysed conditions as no significant effects were found in the ANOVA (luminance contrast: $F(2, 14) = 0.99$, $p = .40$; unipolar mechanism: $F(1, 7) = 2.68$, $p = .15$; interaction $F(1.08, 7.56) = 1.52$, $p = .25$). Reaction times depended on the amount of luminance in the stimulus ($F(1.06, 7.45) = 35.36$, $p < .001$, $\eta_p^2 = .84$), being slowest for isoluminant stimuli ($p = .003$ and $p = .001$), and slower for stimuli with the lower amount of luminance contrast ($p = .043$). No other differences were found (unipolar mechanism: $F(1, 7) = 1.84$, $p = .22$; interaction $F(2, 14) = 0.52$, $p = .60$).

Insert Figure 4 about here

In summary, behavioural performance was reduced for isoluminant stimuli. This effect was more pronounced for bluish than for yellowish targets, while reddish and greenish targets elicited comparable performance.

3.1.2. SSVEP results

We tested the summation of SSVEPs driven by chromatic and luminance signals by implementing a simple model: if the activity for a combined stimulus (e.g., reddish with a higher level of luminance contrast) consists simply of a linear combination of the activity elicited by its constituents (reddish in isolation and higher level of luminance contrast in isolation), then subtracting the combined stimulus response from the sum of the isolating responses should result in a response that is not significantly different from zero. The data differed from this prediction significantly in all cases. The statistical results of this analysis, conducted using the T^2_{circ} statistics of complex amplitudes, are presented in Table 2. From Figure 5, which depicts topographies and complex amplitudes, it is evident that SSVEPs driven by combined chromatic and luminance contrast could not be predicted based on SSVEPs driven by isolated colour and luminance responses. Figure 5 shows that activity elicited by isoluminant stimuli is delayed by approx. 25 ms compared to activity elicited by luminance stimuli. To decompose the latency and amplitude differences in colour/luminance summation between cone-opponent mechanisms, we followed up the T^2_{circ} statistics by separating the difference between observed and predicted (vector sum of isolating responses) data into amplitude and latency and subjecting each separately to a2x2 repeated measures ANOVA (*unipolar colour mechanism* by *luminance contrast).*

Insert Table 2 about here

Insert Figure 5 about here

Insert Figure 6 about here

Amplitude differences for bluish were considerably reduced when compared to those for yellowish ($F(1, 7) = 9.56$,$p = .018$, $\eta_p^2 = .58$). There were no other significant differences (luminance contrast: $F(1, 7) = 1.85$, $p = .22$; interaction: $F(1, 7) = 1.76$, $p = .23$). There was a trend for reduced latency differences for bluish compared to yellowish (main effect of *unipolar colour mechanism* $F(1, 7) = 3.98$, $p = .086$, $\eta_p^2 = .36$). There was also a significant effect of *luminance contrast* ($F(1, 7) = 30.63$, $p = .001$, $\eta_p^2 = .81$), as the magnitude of response latency difference for lower luminance combined with colour was smaller than for higher luminance contrast combined with colour. These effects were further qualified by a significant interaction ($F(1, 7) = 11.22$, $p = .012$, $\eta_p^2 = .62$). We assessed the interaction using paired t-tests with critical p value corrected to .0083. Higher luminance bluish showed more latency reduction than lower luminance bluish ($t(7) = 4.94$, $p = .002$), higher luminance yellowish had more latency reduction than lower luminance yellowish ($t(7) = 5.30$, $p = .001$) as well as lower luminance bluish ($t(7) = 5.77$, $p = .001$), while other differences were not significant.

For the L-M mechanism, amplitude differences for lower and higher luminance contrasts were similar ($F(1, 7) = 2.35$, $p = .17$), and so were amplitude difference for reddish and greenish ($F(1, 7) = 2.69$, $p = .14$). There was no interaction ($F(1, 7) = 0.06$, $p = .81$). The addition of HCFP as a covariate did not alter the observed results significantly (interaction

with colour direction: F(1, 6) = 0.00, p = .97; interaction with luminance contrast: F(1, 6) = 0.13, p = .73; 3-way interaction: F(1, 6) = 0.72, p = .43). Latency differences were again of significantly smaller magnitude for lower as opposed to higher luminance contrast (F(1, 7) = 21.66, p = .002, η_p^2 = .76), with no differences between reddish and greenish (F(1, 7) = 2.81, p = .14) and no interaction (F(1, 7) = 2.62, p = .15). HCFP results did not interact with colour direction (F(1, 6) = 0.11,p = .75) or with luminance contrast (F(1, 6) = 0.14, p = .72) but a 3-way interaction emerged (F(1, 6) = 10.62, p = .017, η_p^2 = .64). We decomposed this interaction by running a linear regression with HCFP results as the predictor for the difference in latency change of higher luminance reddish and greenish vs. the isoluminant condition (Fig. 6b, right panel; the R^2 is equivalent to η_p^2 of the interaction and is significant at the same p value level). As can be seen from the scatterplot in Figure 7, the interaction is driven by the fact that one participant with more efficient luminance processing from reddish than would be predicted by Vλ (negative angles) had faster latency for reddish. In participants whose effective luminance was similar to that predicted by Vλ (i.e., the angle of elevation measured with HCFP was close to 0) latencies were faster for greenish.

It was also important to verify our assumption that at relatively high luminance contrast levels that we employed in our study, the luminance-driven SSVEP would have been saturated in terms of amplitude. In the reddish/greenish experiment, complex amplitudes for lower and higher luminance contrast differed (t2circ = 0.6536, p = 0.02), but this was due to a decrease in latency with higher luminance (Mean difference (std) in milliseconds: -4.80 (1.73); t(7) = -7.87, p < .001) and not due to a change in amplitude (t(7) = -0.37, p = 0.72). The same was the case for the bluish/yellowish experiment: complex amplitudes differed (t2circ = 1.16, p = 0.003) due to a reduction of latency with luminance (Mean difference (std) in milliseconds: -4.00 (1.48), t(7) = -7.62, p < .001) and not due to any changes in amplitude (t(7) = -2.00, p = .09).

Insert Figure 7 about here

3.2 Interim Conclusion: Neural Summation of Colour and Luminance Signals

In summary, activity elicited by a combined colour/luminance stimulus is overwhelmingly not a resultant sum of the activities elicited by colour and luminance respectively. Furthermore, SSVEP amplitudes elicited by S-(L+M) defined stimuli displayed a pronounced asymmetry between bluish and yellowish in terms of their summation with luminance contrast; this was not the case for colours from the L-M mechanism. From Figure 5, it can be observed that luminance-only stimuli elicited very similar amplitudes at both lower and higher luminance contrasts. However, combining them with the same amount of reddish, greenish or yellowish chromatic contrast lead to alterations both in terms of amplitude and in terms of phase, with smaller amplitudes and faster latencies than what would be predicted by a simple additive model. This is indicative of non-linear processing of combined colour and luminance signals.

Speeding up of SSVEP latency is highly dependent on luminance contrast and could therefore also be predicted from individual differences in effective luminance, which we assessed with HCFP. In our sample, the relative contribution of L-cone spectral sensitivity to luminous efficiency changed from relatively high levels to levels that are in line with the approximately 2:1 L/M weighting ratio in Vλ (i.e., nominal isoluminance; Smith and Pokorny, 1975). In line with predictions based on luminous efficiency, one participant whose weighting ratio for L relative to M would have been particularly high had a more pronounced phase advance for reddish. Psychophysically measured phase shifts between L and M cones

have been attributed to subcortical as well as early cortical sites (e.g., Gegenfurtner and Hawken, 1995; Stromeyer et al., 1997). We found an influence of HCFP on SSVEP latency but not on SSVEP amplitude. Similarly, our two relatively high levels of luminance contrast also drove SSVEPs that differed in latency but not amplitude. This has two-fold importance. First, it means that individual differences in Vλ do not need to be accounted for in experiments that only focus on amplitude (for a review of such attentional research, see Andersen et al., 2011). Second, it means that studies that examine the latency of colour-elicited responses, such as the study by Forder and colleagues (2017) may need to take account of individual differences in V_λ to avoid confounding colour-driven responses with luminance-driven responses.

Our second experiment uses the amplitude-based SSVEP feature-selective attention paradigm to assess the possible impact of the asymmetries in joint processing of colour and luminance on selective attention.

3.2. Experiment 2: Selective Attention

In this experiment, participants' task was again to detect brief intervals of 50% coherent motion, but they had to perform it under selective attention demands, detecting coherent motion within the cued, target dots and ignoring any such events within the uncued, distractor dots, as depicted in Figure 3. The purpose of the experiment is to investigate if attentional modulation of neural responses driven by colour-luminance combinations is (1) robust for all colour/luminance combinations and (2) affected by luminance contrast, saturation or both factors. We analysed mean d's, reaction times, AMIs and attentional latency modulation using 2x2x2 repeated measures ANOVAs (behavioural data: attended colour x target luminance contrast x distractor luminance contrast; SSVEP data: colour x colour's luminance contrast x competitor's luminance contrast) and correlational models to

assess whether luminance contrast or saturation are more important in driving attentional effects.

3.2.1. Behavioural results

Figure 8 depicts d's and reaction times (RT), plotted in relation to differences between target and distractor in luminance contrast. It can be seen from Figure 8 that selection of lower luminance bluish in the presence of higher luminance yellowish is significantly below average in terms of d'; meanwhile, selection of higher luminance reddish, greenish and yellowish in the presence of a lower luminance distractor is above average. For RTs, the error bars overlap with the confidence intervals of average performance for all conditions, as the overall differences between them are of much smaller magnitude.

Insert Figure 8 about here

Data were analysed separately by means of a repeated-measures 2x2x2 ANOVA (attended colour x target luminance contrast x distractor luminance contrast) for each of the two directions in colour space. Target and distractor luminance contrast affected behavioural performance in this task in a highly consistent manner for stimuli defined both along the S-(L+M) and L-M cardinal axes. Higher luminance contrast targets were associated with higher sensitivity as reflected by d' (target luminance contrast: S-(L+M): $F(1, 8) = 27.04$, $p < .001$, $\eta_p^2 = .77$; L-M: $F(1, 8) = 27.96$, $p < .001$, $\eta_p^2 = 0.78$) and lower reaction times (target luminance contrast: S-(L+M): $F(1, 8) = 43.06$, $p < .001$, $\eta_p^2 = 0.84$; L-M: $F(1, 8) = 10.07$, $p = .013$, $\eta_p^2 = 0.56$). The opposite pattern occurred for distractor luminance contrast: higher luminance distractors were associated with lower d's (distractor luminance contrast: S-(L+M): $F(1, 8) = 125.50$, $p < .001$, $\eta_p^2 = 0.94$; L-M: $F(1, 8) = 54.79$, $p < .001$, $\eta_p^2 = 0.87$) and higher reaction

times (distractor luminance contrast: S-(L+M): $F(1,8) = 30.54$, $p < .001$, $\eta_p^2 = 0.79$; L-M: $F(1, 8) = 14.55$, $p = .005$, $\eta_p^2 = 0.65$).

In addition to these highly consistent effects, asymmetries in the S-(L+M) mechanism that interacted with luminance contrast were observed. Bluish targets were associated with much lower d' (attended colour: $F(1, 8) = 37.49$, $p < .001$, $\eta_p^2 = 0.82$) and longer reaction times (attended colour: $F(1, 8) = 11.53$, $p = 0.009$, $\eta_p^2 = 0.59$) than yellowish targets. For d', there was also an interaction between target and distractor luminance contrast ($F(1, 8) = 7.29$, $p = .027$, $\eta_p^2 = 0.48$). Tukey's HSD revealed that the sensitivity was highest for higher luminance targets with lower luminance distractors, with all other pairs being similar in terms of d'. The interaction between target luminance contrast and attended colour ($F(1, 8) = 7.61$, $p = .025$, $\eta_p^2 = 0.49$) was such that apart from higher luminance bluish targets and lower luminance yellowish targets producing equivalent performance, all other pairs differed significantly, with lower luminance bluish targets leading to worst performance and higher luminance yellowish targets to best performance. All other main effects and interactions were statistically insignificant ($Fs < 2.49$, $ps > .15$). When chromatic contrasts were defined along the L-M cardinal axis, there was a weak trend for faster performance for reddish ($F(1,8) = 4.03$, $p = .08$), but no other significant effects (all $F<2.04$, all $p<.19$).

In sum, higher target luminance contrast and lower distractor luminance contrast both led to superior performance. For colours from the S-(L+M) mechanism, we also observed both a strong influence of luminance contrast on performance and some asymmetries between bluish and yellowish which resembled those observed in Experiment 1; for colours from the L-M mechanism, luminance contrast was the sole determinant of performance.

We correlated differences between target and distractor in luminance contrast and in saturation with group average d's and RTs, to test which one of these were more important in driving performance. As can be seen from Table 1, colours in our experiment vary not only in

terms of luminance contrast, but also in terms of saturation (calculated as C/L). Figure 8 plots the relation of d' to luminance contrast ($r(16) = 0.922$, $p < .001$) and saturation ($r(16) = -0.195$, $p = .47$). As depicted in Figure 8, RTs also correlated with luminance contrast ($r(16) = -0.895$, $p < .001$), but not with saturation ($r(16) = 0.329$, $p = .21$).

3.2.2. SSVEP results

Mean SSVEP amplitudes are presented in Figure 9, which depicts the topographies and spectra.

Insert Figure 9 about here

Attentional modulation indices (AMIs) and attentional latency modulation were calculated according to equations (1) and (2) to assess if attentional selection of colour at early neural sites reflected by SSVEPs interacts with saturation, luminance contrast, or both. AMIs and attentional latency modulation averaged across participants are depicted in Figure 10, which plots them in relation to saturation and luminance contrast differences between the colour and the competitor colour with which it is presented.

We conducted 2x2x2 repeated measures ANOVAs on AMIs and attentional latency modulation, with the following factors: *colour* (bluish/yellowish or reddish/greenish), *colour's luminance contrast* (lower/higher), and *competitor's luminance contrast* (lower/higher). A colour's luminance contrast had highly consistent effects for stimuli defined both along the S-(L+M) and L-M cardinal axes. Lower luminance contrast stimuli were associated with higher AMIs (S-(L+M): $F(1,8) = 6.04$, $p = .039$, $\eta_p^2 = .43$; L-M: $F(1, 8) = 12.59$, $p = .008$, $\eta_p^2 = .61$). For S-(L+M) direction, this was the only significant finding (all other $F<2.85$, $p>.13$). For the L-M direction, there was also a trend for an effect of competitor's luminance contrast ($F(1, 8) = 4.86$, $p = .059$), which was qualified by a significant interaction between colour's and

competitor's luminance contrast ($F(1,8) = 9.73$, $p = .014$, $\eta_p^2 = .55$): AMIs were larger for lower luminance contrast stimuli in the presence of higher luminance competitors (see Figure 10) compared to the other three combinations of stimulus and competitor luminance contrast. Other results were insignificant ($F<1.99$, $p>.20$).

Surprisingly, the difference in SSVEP latency elicited by stimuli when they were attended as opposed to when they were ignored was generally positive (Fig. 10b), that is the SSVEP response was delayed for attended stimuli. For the S-(L+M) direction there was a difference between bluish and yellowish ($F(1,8) = 7.14$, $p = .028$, $\eta_p^2 = .47$), with attentional latency modulation being more negative for bluish, with no other effects being significant ($F<2.79$, $p >.13$). For L-M direction there was an interaction between colour's and competitor's luminance contrast ($F(1,8) = 6.24$, $p = .037$, $\eta_p^2 = .44$), so that there was a greater slowing of SSVEP responses with attention when the two stimuli had different luminance contrasts. There was also a trend towards a larger attentional latency modulation for reddish than greenish ($F(1,8) = 3.99$, $p = .081$), as well as a trend towards an interaction between colour's and competitor's luminance contrast ($F(1,8) = 3.60$, $p = .094$). No other effects were significant ($F<2.88$, $p >.13$).

Insert Figure 10 about here

We correlated differences between colour's and competitor's (1) luminance contrast and (2) saturation, to test which one of these was more important in driving attentional

selection. AMIs and saturation difference did not correlate ($r(16) = 0.45$, $p = .08$), although there was a weak trend. Luminance contrast difference is negatively correlated with AMIs ($r(16) = -0.676$, $p = .004$). When co-variability of luminance and saturation differences was accounted for in a partial correlation, correlation for luminance contrast differences remained significant ($r(13) = -0.599$, $p = .018$). On the other hand, attentional latency modulation correlated negatively with saturation differences ($r(16) = -0.595$, $p=.015$) and did not relate to luminance differences ($r(16) = 0.138$, $p = .61$). In summary, attentional selection led to an increase in amplitude and (somewhat surprisingly) a slowing of latency for all colours. For the L-M mechanism, stimuli with lower luminance contrast than the competitor benefitted most from attentional amplification, reflected in amplitude increases. Inspection of Figure 10 makes it clear that the lack of this interaction in the S-(L+M) mechanism is probably due to the failure of bluish to be boosted more than average (indicated by the full orange line), with yellowish being highly similar to greenish and reddish. We also replicated findings on asymmetrical cortical summation for bluish - from Figure 9 it is clear that amplitude for bluish again does not depend on its luminance contrast, unlike the other colours.

4. Discussion

In two steady-state visual evoked potential (SSVEP) experiments, we measured behavioural responses and neural activity in response to (1) a single stimulus display and a simple task and a (2) two-stimulus display with the same task performed under selective attention demands. We used stimuli that combined chromatic contrasts originating from different retinogeniculate mechanisms with varying levels of positive luminance contrast. First, we investigated colour contrast only, luminance contrast only, and combined contrast performance and SSVEPs to assess signal summation without manipulating attention. Subsequently, we investigated performance and SSVEPs for combined contrast stimuli under

selective attention demands. First, we found that neural summation could not be modelled as an outcome of two independent colour and luminance-derived signals - a finding that was replicated in the second experiment. Elicited amplitudes were generally of much smaller magnitude than one would have expected from independent vector summation of chromatic and luminance signals, although this interaction was much reduced for bluish. In addition, the phases (latencies) elicited by combined colour-luminance stimuli were closer to the phase of the luminance only stimuli than would have been expected from independent vector summation. This effect was comparable for all four colours and corresponded to an advance of the cortical response by roughly 5-10 ms. Second, voluntary selective attention exhibited different effects depending on the difference in luminance contrast between the two superimposed stimuli. SSVEP-derived AMIs were larger for colours that were lower in luminance contrast. Attentional increases for stimuli lower in contrast would be consistent with contrast gain modulation. Further, for reddish and greenish, attentional effects, as reflect in AMIs, were maximal for lower luminance contrast colours in the presence of higher luminance contrast competitors. Surprisingly, latencies were found to be slower for attended than for unattended colours. Previously, spatial attention was reported to speed up the latency for luminance-defined stimuli, but not for isoluminant stimuli (Di Russo et al., 2001), which was taken as indicative of different attentional mechanisms for achromatic and chromatic signals. Our experiment on feature-based attention finds latency slowing for attended stimuli that combine colour and luminance contrast. Since our summation experiment found slower latencies for isoluminant and combined colour/luminance than for luminance-only stimuli, this may be indicative of selective attention targeting the chromatic and the achromatic component of the stimulus differentially in order to achieve attentional amplification.

Considering these findings, we conclude that colour and luminance are processed jointly, with bluish being the odd colour in terms of cortical summation and attentional

modulation: SSVEP amplitudes elicited by bluish stimuli show less interaction with luminance and attentional selection of such stimuli is less robust. SSVEP indices of selective attention to colour demonstrate that luminance contrasts of both targets and distractors are important determinants of feature-based selection at the earlier stages of visual processing. As SSVEPs for joint colour and luminance stimuli are mainly driven by cortical sources that combine the two types of signal in a non-linear fashion, this implies that these neural sources make a contribution that is crucial both for perception and attentional selection.

While behavioural performance depended very linearly on luminance contrast differences between targets and distractors, increases in AMIs were most pronounced for lower luminance contrast targets. We observed similar discrepancies between behavioural and neural-level data in our previous study on bottom-up biases in selective attention due to differences in luminance contrast (Andersen et al., 2012): in that experiment, the attended stimulus could also neurally "lose" competition in the visual cortex but still effectively control behavioural responses. In the present study, when concurrently presented and competing for attention, stimuli that were lower in luminance than distractors received more attentional modulation in the areas of the visual cortex that gave rise to our SSVEPs (V1-V3), while processing at a later stage (e.g., motion sensitive visual areas and decision-related higher-level cortical areas) nevertheless lead to more efficient behavioural performance for stimuli of higher luminance than distractors, with costs for targets lower in luminance than distractors. This confirms that distinct stimulus saliences are likely to be computed concurrently in the visual cortex, with those saliences that are task-relevant (in our case that would be coherent motion salience) impacting more strongly on behaviour. These findings are inconsistent with the "integrated competition hypothesis," which assumes that the same stimulus "wins" competition across all levels of the processing hierarchy (Duncan et al., 1997). Motion processing is predominantly reliant upon luminance contrast (for a review, see Cropper and Wuerger, 2005), thus higher

luminance stimuli can carry a stronger motion signal than the corresponding lower luminance stimuli despite being less salient at earlier processing stages. Inhibition from brightness to colour signals, leading to desaturation, has been argued to result from inhibitory colour brightness interactions in V1 (Xing et al., 2015). Nagy and Sanchez (1992) were puzzled by their observation that visual search benefited from combining luminance differences with chromaticity differences only when the target was dimmer than the distractors. However, their observation is perfectly in line with our own SSVEP findings and conforms to the contrast gain modulation of neural activity. In contrast to early areas, which are highly responsive to both colour and luminance contrast, higher luminance contrasts which lead to larger motion signals would be expected to predominate in motion processing areas of the cortex such as MT. This is consistent with Andersen et al.'s (2012) findings that attentional selection multiplicatively enhanced SSVEPs at central occipital electrodes, which mainly reflect V1-V3 sources, with an additive effect at more lateral parieto-occipital sites, which mainly reflect MT sources. Thus, different stimuli can "win" the competition at different levels of the processing hierarchy and which stimulus dominates the competition for control of behaviour depends on which stimulus properties that behaviour is based upon. Feature-based attention is hypothesised to play a role in storing an active representation of the target throughout the task (Chelazzi et al., 2001; Hayden and Gallant, 2005; Motter, 1994), which is perhaps why its effects are reflected so effectively in SSVEP indices of sustained selective attention. In terms of neurophysiological mechanisms, attentional modulations of SSVEP amplitudes after the presentation of a static colour cue could be particularly sensitive to baseline shifts in early visual areas, as reported by Cutrone et al. (2014) and consistent with the work of Sani and colleagues (2017). Additional processing stages and putative attentional modulations at these later stages would subsequently combine with the early effects to lead to overt behaviour.

Bluish was associated with lower performance in our experiments. Lindsey et al. (2010) report the same. When presented as a single stimulus in the first experiment, S-(L+M) signals summed asymmetrically with luminance. Bluish did not show the same non-linear integration with luminance which resulted in lower amplitudes than predicted from independent vector summation for the three other colours (Fig. 6; also see Figure 9 for the same finding in the attentional experiment). Rather, the amplitudes driven by bluish and by luminance contrast seemed to be more independent of each other. Cottaris and DeValois (1998) reported that V1 cells with S-cone inputs had less stable chromatic tuning over time and longer response latency. S-cone signals go through a longer and more active stage of processing before exerting maximal impact on V1 cells, with the likely candidate for this stage being the recurrent excitatory network which is thought to be responsible for the amplification of the S-cone signals in V1 (De Valois et al., 2000; for a review, see Xiao, 2014). Human fMRI shows that such amplification results in relatively equal cortical activity for bluish in spite of the much weaker subcortical S-cone signal (Mullen et al., 2008). The need to amplify S-cone signals in a separate recurrent network may be the potential source of the observed asymmetries in cortical summation as well as the observed failure to achieve additional above-average attentional amplification of the signal due to luminance contrast differences between target and distractor. This should be directly investigated in studies on primates or through neural network models, to assess if two-fold contrast-dependent amplification of the same signal can be achieved in V1.

Finally, the dependence of attention effects on both stimulus chromaticity and luminance is clearly different from the pronounced independence of attentional selection between different feature dimensions in previous studies (e.g., colour and orientation, see Andersen et al., 2008; Andersen et al., 2015). Thus, dimensions in colour space are not treated as separate feature dimensions for attentional selection. At the same time, they cannot be

considered a single unified feature dimension either, as selective attention in our study seems to be targeting the relatively slower chromatic component of the stimulus more strongly, resulting in the counter-intuitive finding of slower SSVEP latencies elicited by attended stimuli. This leads us to conclude that colour and luminance are interdependent, both in terms of perception and in terms of attentional selection, with a potential candidate mediating their link being stimulus appearance, which depends on both chromaticity and luminance.

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Figures

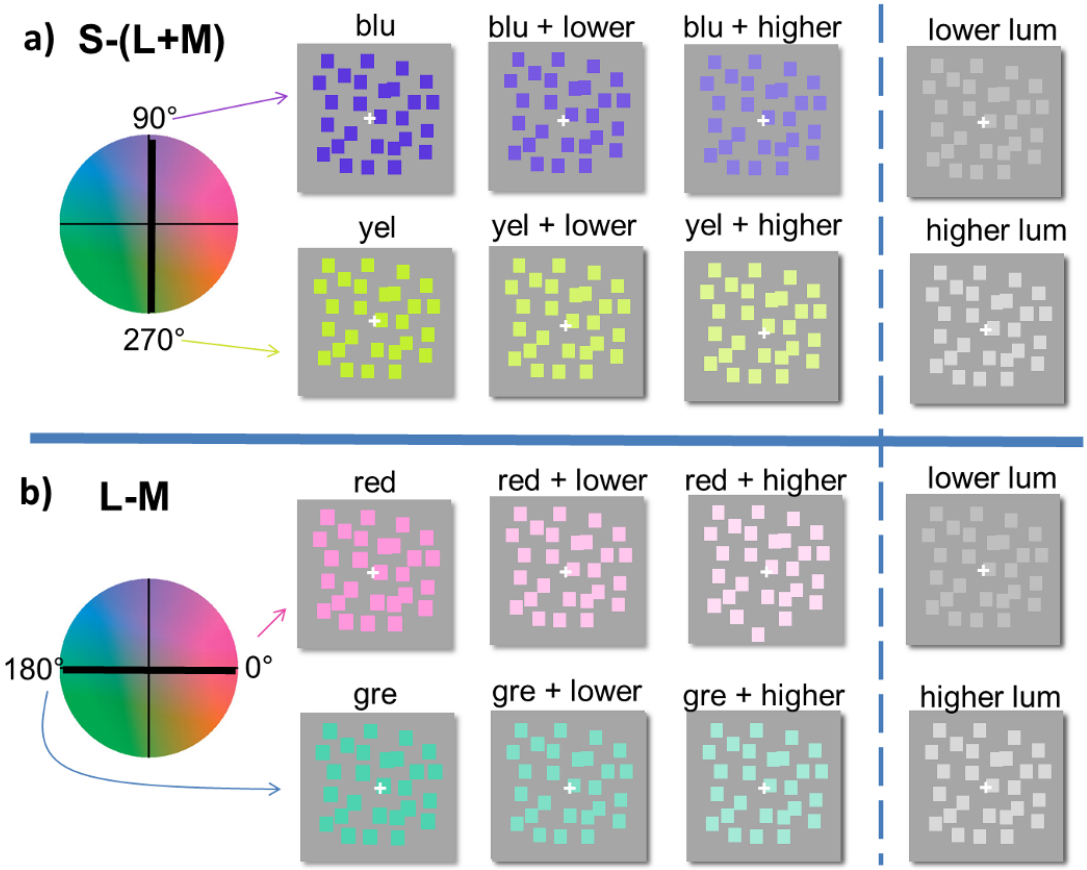

Figure 1*: Stimuli for experiment 1 (summation).** *A single frame of the random dot kinematogram is shown, with the number of dots reduced for the sake of clarity. An isoluminant plane of the DKL colour space is shown next to it, with the two orthogonal chromatic mechanisms depicted: S-(L+M) mechanism, with its vertical axis incorporating the increment (bluish; 90°) and the decrement (yellowish; 270°) colours, and the L-M mechanism, with its horizontal axis incorporating the increment (reddish; 0°) and decrement (greenish; 180°) colours. Colours represent increments and decrements relative to the centre of the DKL space, the so-called "white point", which was used as the background.* ***A) *In the first session of the experiment, stimuli either isolated increments and decrements along the S-(L+M) chromatic axis or combined them with two luminance increment levels (a lower and a higher level).* ***B)*** *In the second session of the experiment, stimuli isolated increments and decrements along the L-M axis or combined them with two luminance increment levels. Both experiments also included*

achromatic stimuli at the lower or higher luminance increment level. The dots flickered at 10 Hz thus driving SSVEPs.

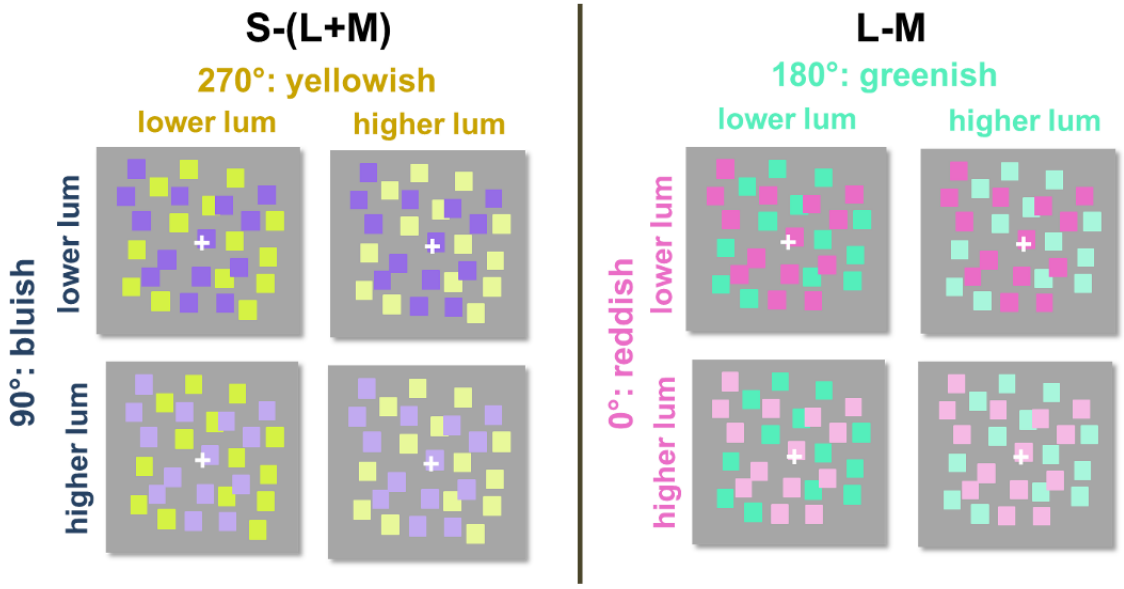

Figure 2: Stimuli for experiment 2 (attention). *An example of a single frame of the random dot kinematogram is shown, with the number of dots reduced for the sake of clarity. In the first session of the experiment (left panel), stimuli combined increments and decrements along the S-(L+M) chromatic axis with one of two luminance increment levels. In the second session of the experiment (right panel), stimuli combined increments and decrements along the L-M axis with one of two luminance increment levels. During the motion interval increments flickered at 10 Hz, whilst decrements flickered at 12 Hz, driving SSVEPs.*

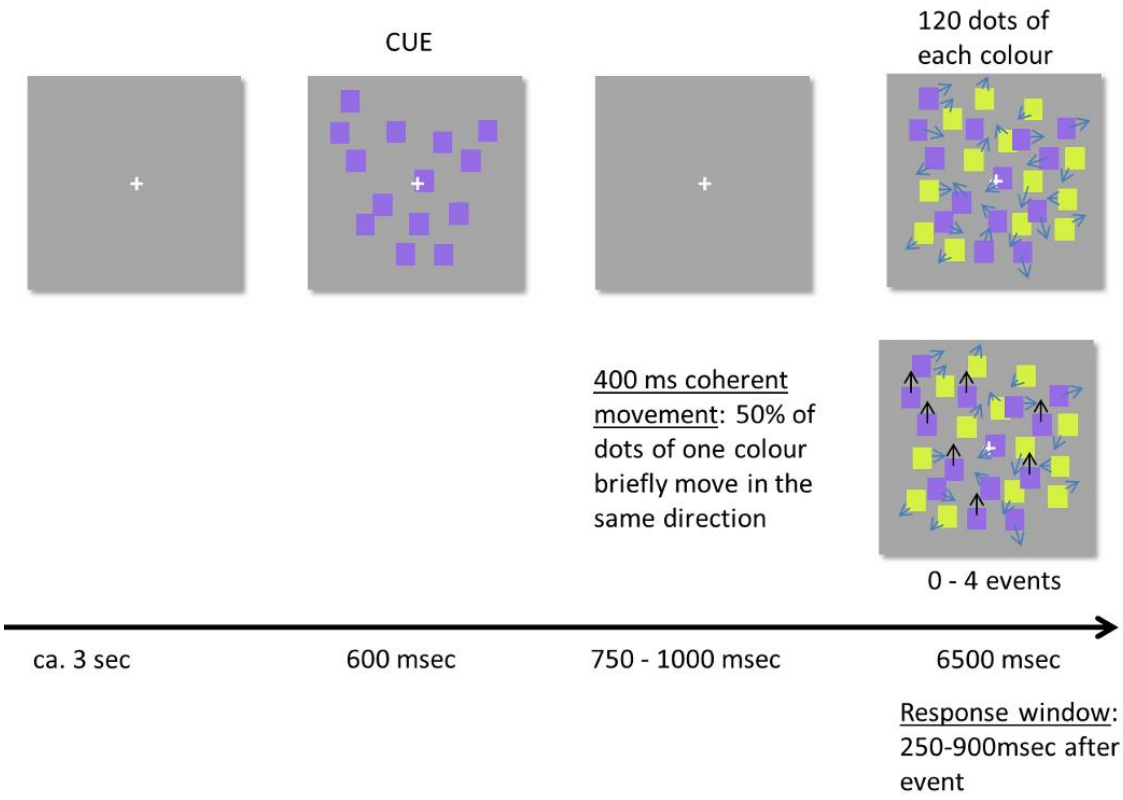

Figure 3. Trial outlook for Experiment 2 (attention). *Participants were cued to attend to a colour and subsequently observed the moving and flickering dots for 6500ms. During this time, between 0 and 4 brief coherent motion intervals could occur. Participants responded with a button press to coherent motion (targets) in the attended colours whilst refraining to respond to coherent motion of the unattended colour (distractors). In experiment 1 (summation), the trial outlook was highly similar: participants still received a cue, but they then observed a RDK that consisted only of dots of a single colour, performing the same motion detection task without the selective attention demands. The number of dots depicted here is reduced for the sake of clarity.*

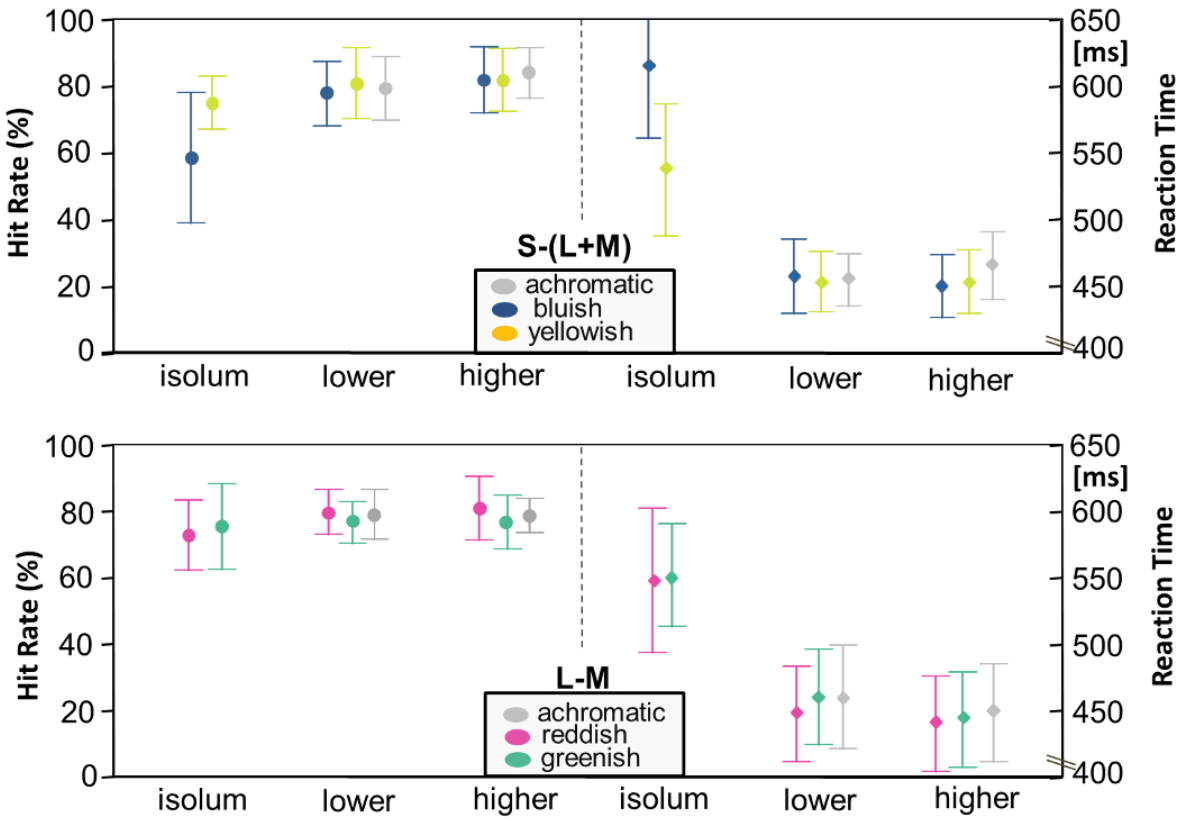

Figure 4. Experiment 1 (summation): behavioural data. *The top panel depicts the hit rates and reaction times from the S-(L+M) session, whilst the lower panel depicts the L-M session. To facilitate comparisons, both hit rates (left, circles) and reaction times (right, diamonds) are plotted adjacent to each other. Error bars +/- 2 SEs.*

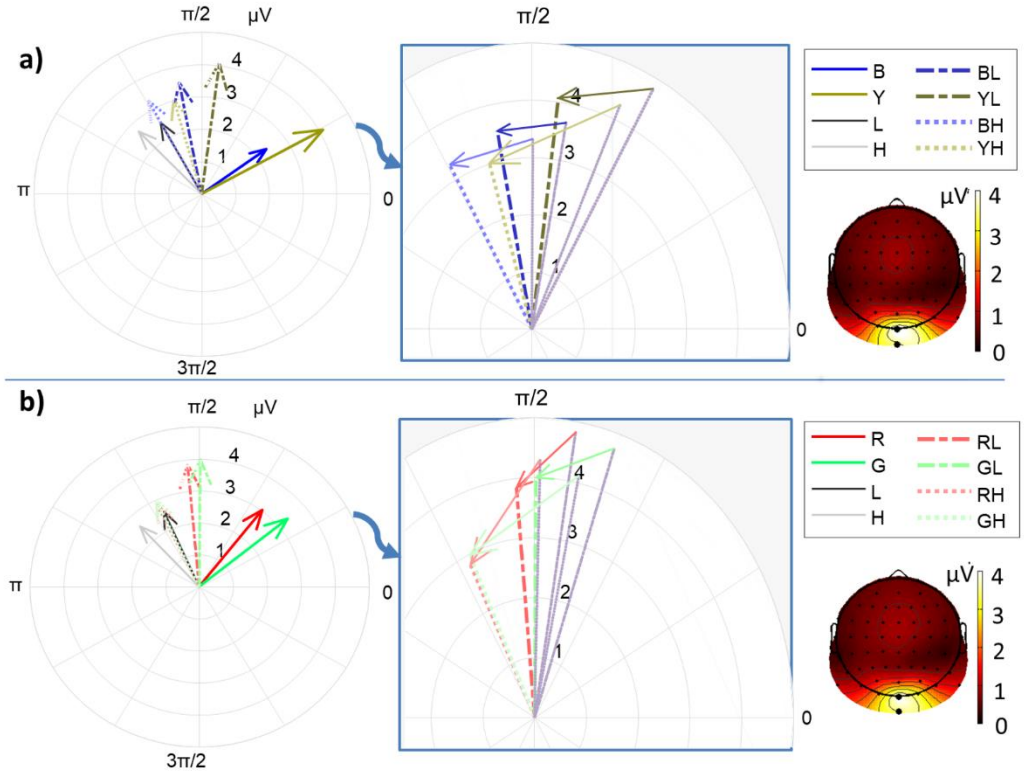

Figure 5. SSVEPs elicited by colour-isolating, luminance-isolating and combined colour/luminance stimuli. a) S-(L+M) and luminance contrast; b) L-M and luminance contrast*. Topography of SSVEPs (on the right), collapsed across all conditions, indicates an occipital peak in activity focused around electrodes Oz and Iz. Mean phases (angle of arrows) and amplitudes (length of arrows) at these electrodes are depicted in polar plots that occupy the centre of the Figure. Differences in phase between isolated colour-driven responses (thicker, full lines) and luminance-driven responses (thinner full lines) are vast. Responses to combined colour/luminance stimuli appear to be closer in phase to luminance-isolating than to colour-isolating stimuli. The light grey rectangles superimposed over the polar plots indicate an area in which the observed SSVEP responses are concentrated. Right of the polar plots, a magnified view of this area is shown, highlighting that summation of colour and luminance cannot be reduced to an additive combination of colour and luminance: the thin purple lines in these magnified views correspond to an additive prediction of SSVEPs, while the thicker, colour-coded lines represent the observed data as already depicted in the polar plots. The full*

lines connect the predictions and observations with the arrow pointing towards the observed data, highlighting the differences in phase and amplitude and thus illustrating the statistical tests presented in Table 2. In all cases, with higher luminance contrast the phase approaches that of the luminance isolating stimulus. As the stimulus flickered at 10 Hz, each quadrant of the phase circle is equivalent to 25 ms. More insight into summation of colour and luminance can be obtained from Figure 6, which presents bar plots of amplitude and phase differences between observed SSVEPs and the SSSVEPs predicted fromadditition, which are also depicted in the magnified sections of the polar plots here.

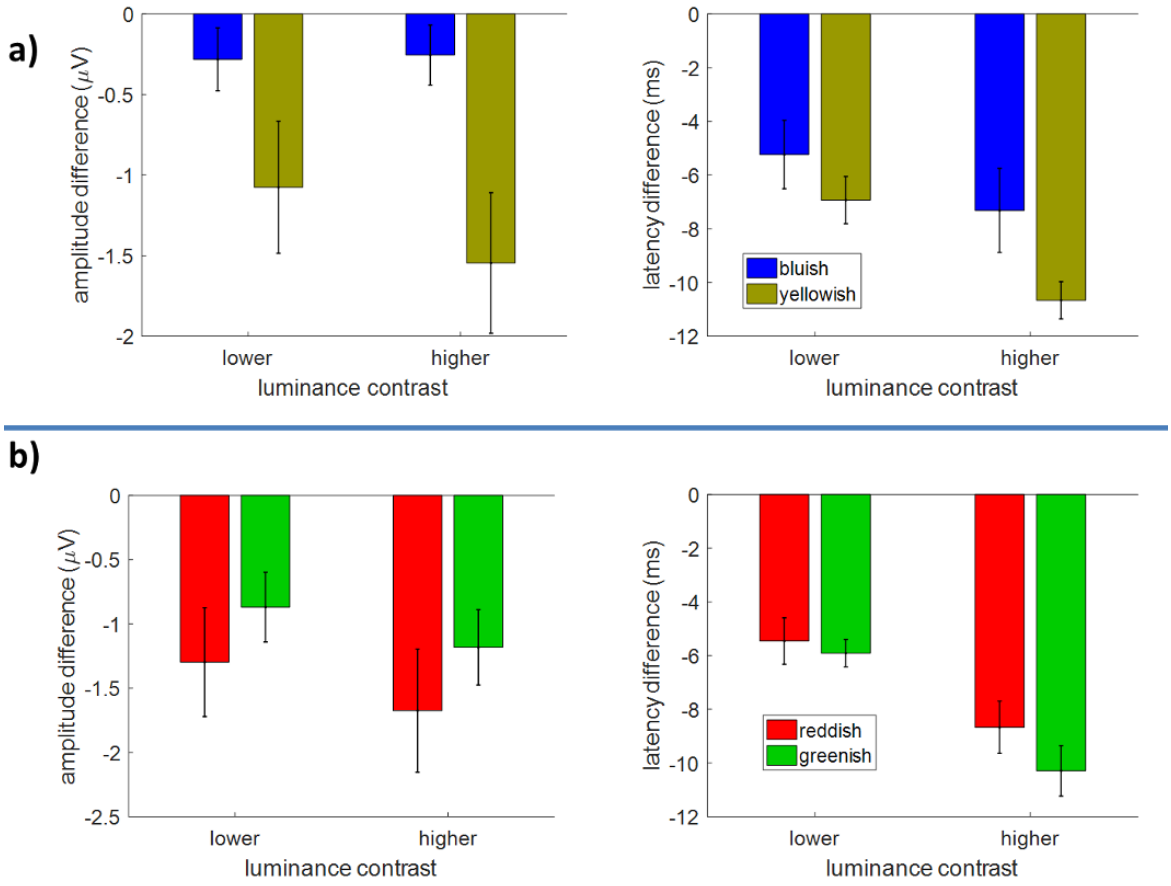

Figure 6. Bar plots of differences in amplitude and phase between SSVEPs observed in response to combined colour and luminance contrast and predictions based on a simple additive model of colour and luminance SSVEPs. *This bar plot decomposes amplitudes and phases of SSVEPs (see Fig. 5 for further detail). Combinations of colour with luminance contrast drive a higher amplitude of the response (with the exception of bluish at a lower*

luminance level) and a faster latency of the response. Asymmetries are observed between bluish and yellowish, but not between reddish and greenish. Error bars are +/- 1 SEM.

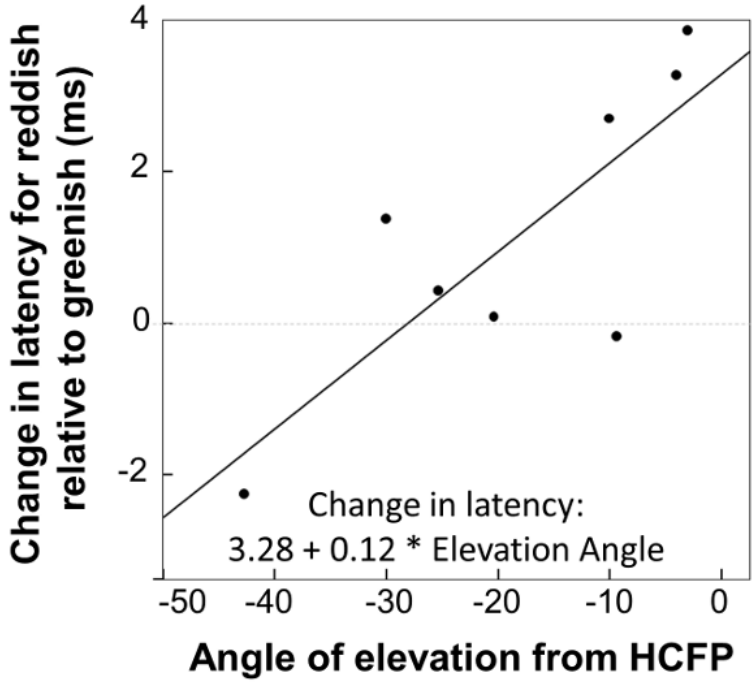

Figure 7. Individual variability in effective luminance of reddish/greenish as measured with HCFP predicts differences between these two colours in the speeding up of phase with increased luminance contrast. *The x axis represents angle of elevation in DKL colour space as measured with HCFP. At zero, effective luminance is well represented by Vλ. Negative values indicate that L cones weighting is higher than in Vλ, which would require reddish to be brighter and greenish to be darker than the background to achieve isoluminance. The y axis represents the differences between reddish and greenish in the speeding up of phase for higher relative to lower luminance contrast. Positive values indicate more speeding up for reddish, while negative values indicate more speeding up for greenish. The regression function is presented at the top of the graph.*

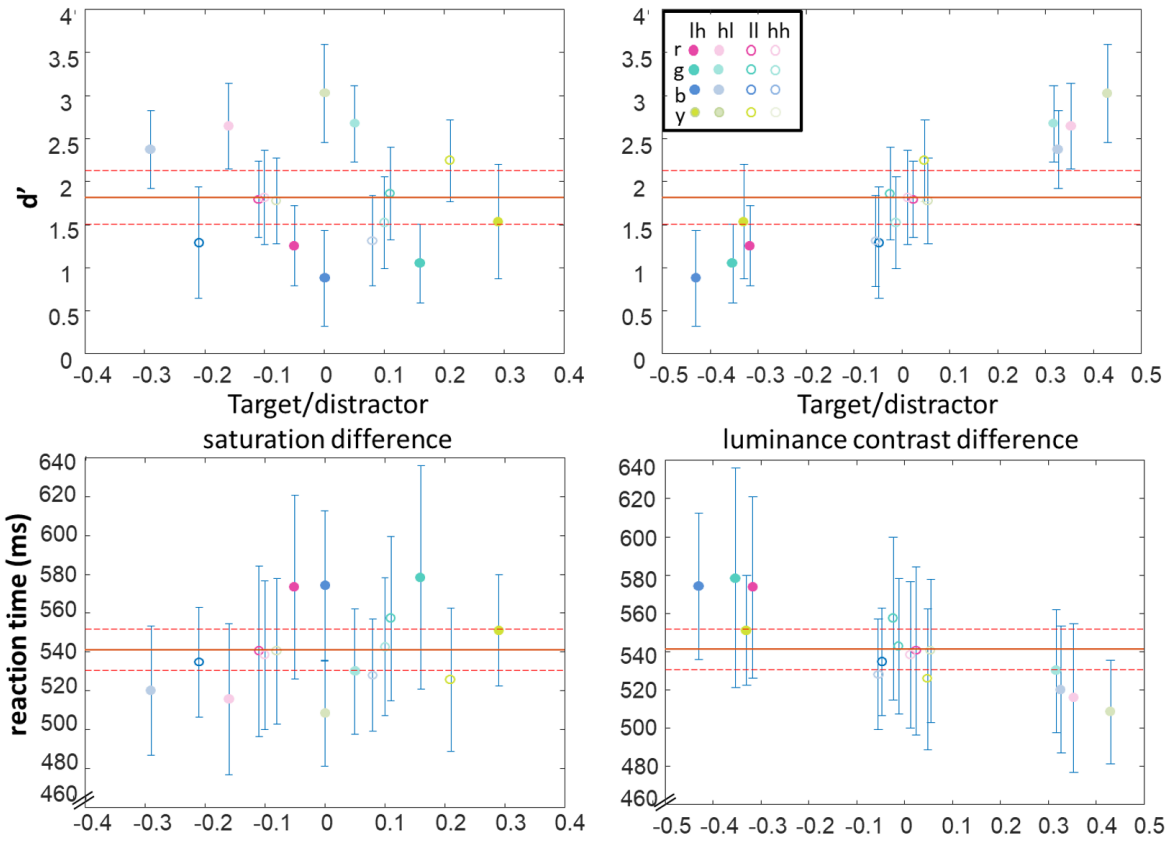

Figure 8. Experiment 2 (attention): behavioural data*. The top panel depicts the d's and the bottom panel depicts the reaction times Both are plotted against stimulus saturation (left) and luminance contrast (right). Error bars +/- 2 SEs.*

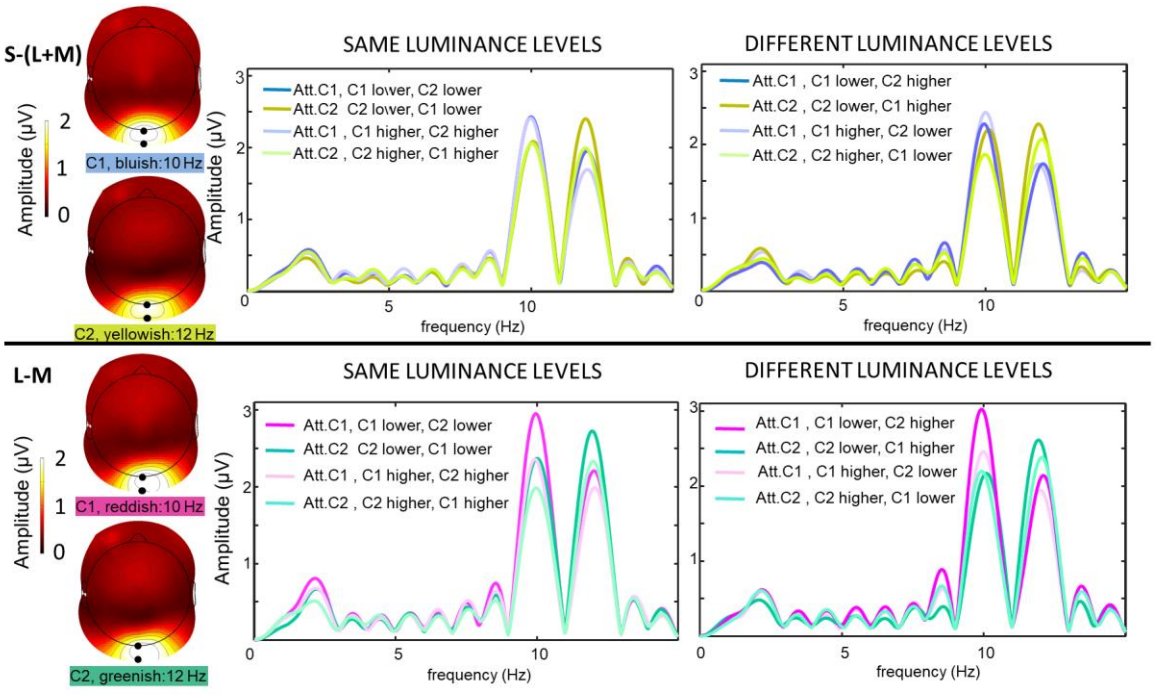

Figure 9. Spectra and topographies for Experiment 2 (attention). *Amplitudes of SSVEPs for S-(L+M) and L-M conditions are presented on sub-panels containing responses elicited at same and different target and distractor luminance contrast levels. Topographies are presented collapsed across all conditions for bluish, yellowish, reddish and greenish.*

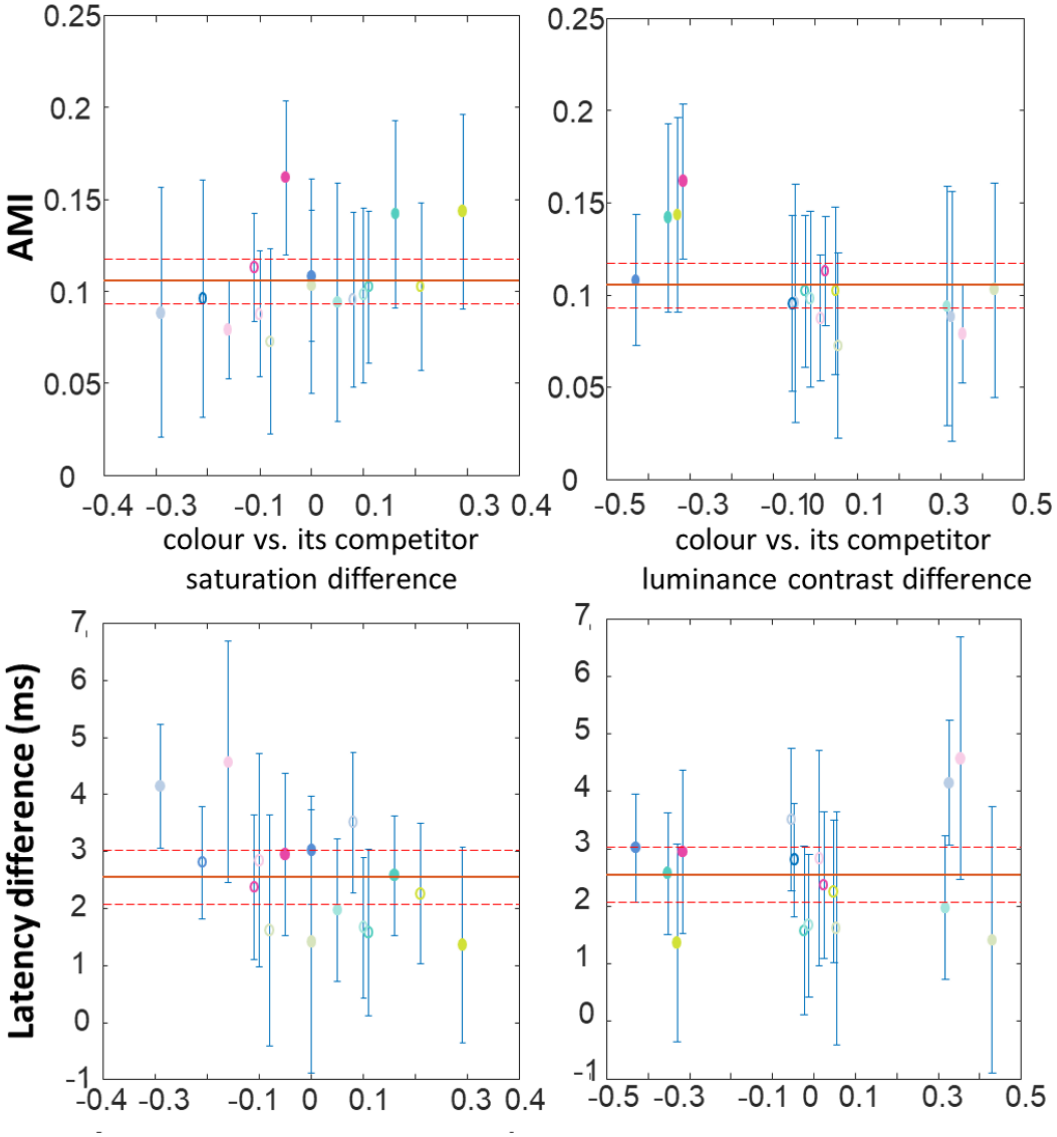

Figure 10. Attentional modulation indices (AMIs). *Top panel depicts AMIs while bottom panel depicts attentional latency differences for all colours. Attentional modulations are plotted against stimulus saturation (left) and luminance contrast (right). Error bars: +/- 2 SEs.*

Tables

Table 1. *CIE 1931 and CIE Lch coordinates of the colours used in the experiments.*

	CIE 1931			CIE Lch				Contrast		
	x	y	Y	L	c	h	c/L	L-M	2S-(L+M)	Lum
isoluminant bluish	0.27	0.23	43.6	72.0	48.1	305.1	0.67	0.004	0.820	-0.018
isoluminant yellowish	0.38	0.52	45.0	72.9	74.6	115.5	1.02	-0.006	-0.847	0.015
isoluminant reddish	0.36	0.30	45.8	73.1	31.1	356.2	0.43	0.171	-0.021	0.032
isoluminant greenish	0.24	0.35	44.7	72.7	39.6	185.5	0.54	-0.177	-0.045	0.007
Lower luminance	0.30	0.33	61.0	82.4	6.5	194.9	0.08	-0.007	-0.041	0.375
Higher luminance	0.30	0.33	75.5	89.6	6.9	194.9	0.08	-0.008	-0.067	0.702
Bluish at lower lum	0.28	0.26	59.0	81.3	34.4	301.2	0.42	-0.003	1.507	0.330
Yellowish at lower lum	0.35	0.45	61.2	82.5	51.7	122.0	0.63	-0.003	1.690	0.378
Bluish at higher lum	0.28	0.27	75.7	89.7	30.9	295.8	0.34	-0.002	1.44	0.705
Yellowish at higher lum	0.34	0.41	78.1	90.8	38.3	122.3	0.42	-0.005	-1.677	0.760
Reddish at lower lum	0.34	0.31	62.0	82.9	20.9	354.3	0.25	0.175	-0.011	0.397
Greenish at lower lum	0.26	0.34	61.0	82.4	30.0	188.5	0.36	-0.175	-0.041	0.373
Reddish at higher lum	0.33	0.31	76.6	90.1	18.1	347.3	0.20	0.171	0.006	0.726
Greenish at higher lum	0.27	0.34	76.0	89.9	26.7	186.9	0.30	-0.175	-0.040	0.714

Note: transformation into CIE Lch was done using d65 illuminant and CIE 1931 2° colour matching functions.

Table 2. Results of the statistical tests of the predicted complex amplitudes for combined colour/luminance contrast stimuli.

Color/luminance combination	**$T^2_{circ}(14)$ for difference from 0**	**p value**
Darker bluish (S-(L+M) Increment, Lower Luminance)	1.36	<0.001

Lighter bluish (S-(L+M) Increment, Higher Luminance)	1.21	<0.001
Darker yellowish (S-(L+M) Decrement, Lower Luminance)	0.93	<0.001
Lighter yellowish (S-(L+M) Decrement, Higher Luminance)	1.28	<0.001
L-M:		
Darker reddish (L-M Increment, Lower Luminance)	0.60	0.03
Lighter reddish (L-M Increment, Higher Luminance)	0.79	0.01
Darker greenish (L-M Decrement, Lower Luminance)	0.89	0.007
Lighter greenish (L-M Decrement, Higher Luminance)	1.22	0.002