

Neural mechanisms of divided feature-selective attention to colour

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Abstract

Feature-based attentional selection of colour is challenging to investigate due to the multidimensional nature of colour-space. When attending concurrently to features from different feature dimensions (e.g. red and horizontal), the attentional selections of the separate dimensions are largely independent. Therefore, if colour constitutes multiple independent feature dimensions for attentional purposes, concurrently attending to two colours should be effective and independent of the specific configuration of target and distractor colours. Here, observers attended concurrently to two out of four fully overlapping random dot kinematograms of different colours, and the allocation of attention to each colour was assessed separately by recordings of steady-state visual evoked potentials. The magnitude of attention effects depended on colour proximity and was well described by a simple model which suggested that colour space is rescaled in an adaptive manner to achieve attentional selection. In conclusion, different spatially overlaid colours can be attended concurrently with an efficiency that is determined by their configuration in colour space, supporting the idea that (at least in terms of hue) colour acts as a single dimension for attentional purposes.

Keywords: color vision, SSVEP, feature-based attention, target proximity, linear separability

1. Introduction

Attentional selection is essential for adaptive visually guided behaviour. In simple scenes, selection might be achieved by attending to a single target-defining feature of an object, e.g. its spatial location, colour, orientation or direction of motion. However, in more complex scenes, it is often necessary to select a behaviourally relevant stimulus which differs from its surroundings along multiple dimensions (e.g. a red object moving leftwards) or along multiple feature values belonging to a single dimension (e.g. a red and green object). Therefore, understanding how attentional mechanisms work together to achieve such selection is essential. Recent studies have delineated the neural mechanisms of concurrent attention to spatial location and colour (Andersen et al., 2011a) and colour and orientation (Andersen et al., 2008; Andersen et al., 2015) and found these selection processes to operate in a largely parallel and independent manner. These findings are compatible with and extend established models of visual attention (Bundesen, 1990; Treue and Martinez-Trujillo, 1999).

Attention can also be concurrently applied to colours at different spatial locations, although a loss of feature selectivity results when distractors that share target chromaticity are positioned in the unattended location (Andersen et al., 2013). However, it remains unknown how concurrent attention to two colours may be achieved and neurally implemented. For attentional purposes, colour might be conceptualised either as a unitary, continuous feature dimension or, alternatively, as a dimension that can be further subdivided into subdimensions representing colour categories (e.g. red or blue; see Found and Muller, 1996) or dimensions of colour space (lightness, saturation and hue; see Sun et al., 2016). Consider the situation in which attention is paid simultaneously to two colours that are equal in saturation and

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lightness but different in hue. The critical question is whether attention would lead to a simultaneous enhancement of the two discrete colours (e.g., red and blue) or, alternatively would it lead to an enhancement of a continuum of intermediate values between them (e.g., red to blue, including purple). In the first case, attention would be divided between different values in feature space. If the efficiency of such attentional selection was found to be largely independent of the specific combination of colours being attended, this would support accounts of multiple sub-dimensions based on colour categories, as suggested by Found and Muller (1996). In the second case, attention would be generalized to encompass all colours in the relevant range. The efficiency of attentional selection would then depend upon the distance of the attended colours in colour space and would be consistent with the neuroscientific evidence that hue tuning of proximal cortical neurons tends to overlap in macaque V1 and V2 (Xiao et al., 2007; Xiao et al., 2003), and that in humans a perceptual colour space in which proximal neurons code neighbouring hues can be seen in V4 and VO1 (Brouwer and Heeger, 2009). Such a pattern would be most consistent with the idea of colour as a single attentional dimension.

The present study aims to investigate the neural implementation of divided attention to colour, so it is paramount to consider the way in which colour is represented in the brain. Colour is first represented by sub-cortical cone-opponent mechanisms; these signals are then recombined by cortical colour-opponent mechanisms, with a yet further categorical level of representation evidenced by colour naming (for a review, see Stockman and Brainard, 2010). Neurons in the lateral geniculate nucleus (LGN) are tuned to the two orthogonal cone-opponent mechanisms while in the cortex neurons exhibit preferential responses to a much

larger number of hues (Gegenfurtner, 2003; Parkes et al., 2009), with the predominant tuning shifted away from the axes of the cone-opponent mechanisms, possibly with a slight dominance towards colour directions aligned with perceptual hues of blue/yellow and red/green in extrastriate areas (Conway and Stoughton, 2009; Mollon, 2009; Stoughton and Conway, 2008). Multivariate analyses of human fMRI responses revealed that encoding of colour is distributed and that colour-selective neurons have relatively broad and overlapping tuning curves (Brouwer and Heeger, 2009; for complementary evidence from macaque V1, V2 and V4 see Tanigawa et al., 2010; Xiao et al., 2007; Xiao et al., 2003). In human fMRI studies, perceptual and categorical representations of colour were reliably identified only in extrastriate areas V4 and VO1, even though earlier areas (e.g., V1) were also robustly activated by colour (Brouwer and Heeger, 2009, 2013). Thus, cortical neurons in a range of visual areas (from V1 to V4/VO1) represent the most likely candidates for mediating the simultaneous selection of multiple colour targets in the presence of chromatic distractors.

Based on this, target-distractor and distractor-distractor distances in colour space are an important determinant of visual search efficiency both when searching for a single target or for multiple targets, while target-target distances become important when multiple targets are present (Nagy and Sanchez, 1990; Stroud et al., 2012). Targets that are closer to each other and further away from the distractors are selected more efficiently. But there are additional factors that may affect the simultaneous selection of multiple colour targets. The linear separability model predicts costs associated with simultaneous selection of target colours that are not separable from distractor colours by a single line in colour space, due to the difficulty of filtering out distractors that are positioned in-between the targets (Bauer et

al., 1996; Bauer et al., 1998, 1999; D'Zmura, 1991). When targets are not linearly separable from distractor(s), visual search changes from parallel to serial, i.e. becomes less efficient. Efficient selection account of attention (Pestilli et al., 2011) might argue that the in-between distractor prevents the selection of only the behaviourally-relevant signals that are associated with the targets, instead enforcing an obligatory pooling of signals which encompass both the target colours and distractor colour(s). The resultant large variance in the neural response dilutes the response differences between stimuli, thus reducing stimulus discriminability. When multiple targets are to be attended, the linear separability effect could thus influence attentional selection over and above the well-known, classical effects of colour differences.

The visual search paradigm has provided much evidence on colour selection, but it is not an ideal tool for investigating the neural mechanisms of attentional selection of colour *per se*. This is because visual search always includes a spatial component, with items of different colours occupying different spatial locations in the display. Therefore, visual search experiments cannot distinguish direct attentional selection within a feature dimension (here, colour) from the role of features in guiding spatial attention to a location (Andersen et al., 2009; Shih and Sperling, 1996; Vierck and Miller, 2008). Relatively recently, feature selection paradigms have been developed to look more closely at the neural markers of non-spatial attentional selection such as selection of colour. One of these is the feature-based steady-state visual evoked potential (SSVEP) paradigm (Andersen et al., 2011a; Andersen et al., 2008; Andersen and Muller, 2010; Andersen et al., 2009; Andersen et al., 2012; Müller et al., 2006). In this paradigm, behavioural measures (e.g., hit rates, false alarms, reaction times) can be taken concurrently with measures of target and distractor processing in the visual

cortex derived from frequency-tagged SSVEP amplitudes. Feature-based attentional selection has been studied using displays with continuously moving, overlapping random dot kinematograms (RDKs). Because the arrays of dots having different features move and overlap randomly, while occupying the same area of space, there is no spatial or depth separation to differentiate them. If each set of dots flickers at a different frequency, they will drive distinct SSVEPs, and thus the neural response driven by each of the overlapping arrays of differently coloured dots can be monitored independently. Attention to a stimulus selectively enhances the amplitude of the SSVEP at its flicker-frequency in the visual cortex (Morgan et al., 1996; for a review see Andersen et al., 2011b). The cortical sources of attentional modulations of SSVEPs driven by fast flicker in the above-mentioned feature-based paradigm are mainly in the posterior occipital lobe region that includes both striate and early extrastriate areas (Müller et al., 2006; Andersen et al., 2008). Therefore, SSVEP recordings provide a way to study how attention modulates early cortical representations of different features, supplementing traditional behavioural indicators of attentional selection.

In the present study, we used the feature-based SSVEP attention paradigm with a task that required attention to be divided between two colours in a four-colour display. The primary aim was to establish whether it is possible to divide early neural attentional resources between two feature values within colour space. The secondary aim was to establish whether the early neural implementation of concurrent attention to separate colours depends on the same factors identified in previous behavioural studies – that is, target-target and target-distractor colour differences (Nagy and Sanchez, 1990), linear separability in colour space (Bauer et al., 1996; D'Zmura, 1991), or a combination of both. We conducted two

experiments, one with four unique hues, and one with a combination of unique and intermediate hues. Colour selection was assessed in these two different contexts to investigate the separate influences of colour distance and linear separability in colour space on the efficiency of attentional selection. The properties of these two contexts were as follows: (1) in experiment 1, stimuli were set to unique hue values taken from a normative study (Wuerger, 2013; Wuerger et al., 2005) and thus fell on the axes of a perceptual hue space (red-green and blue-yellow; as in D'Zmura, 1991); and (2) in experiment 2, stimuli were set to a mix of unique and intermediate hues, in which a unique hue from each axis of the perceptual colour space (red; blue) was accompanied by an intermediate hue. One of the intermediate hues was interpolated to fall half-way between the two unique hues (purple) and the other was interpolated to fall on the opposite side of the colour space (lime). Thus, in one colour context there were four colours that were more spread across the perceptual colour space (red, blue, green, yellow), while in the other colour context there were three colours in a narrower area of perceptual colour space (red, purple, blue) with one colour further away (lime). While our stimulus colours were selected from normative unique hue data collected by Wuerger and colleagues, the differences between the two experiments (red, green, blue and yellow vs. red, purple, blue and lime) in terms of relative colour distances hold across all perceptual colour spaces, including Munsell, CIELAB and CIELUV (C.I.E., 2018). Furthermore, due to the good inter-observer consistency in unique hue settings in the normative studies of Wuerger and colleagues, we could be fairly sure that the hues in our experiments would be relatively good representatives of their respective categories (red, blue, green, yellow, purple and lime). The two chosen configurations of colours allowed us to robustly test (1) if attention-related magnification of SSVEPs is possible when concurrently

selecting two colours; (2) if this effect depends on colour distances and/or linear separability between targets and distractors.

2. Materials and Methods

2.1 Participants

Experiment 1 (red, blue, green, yellow) included 12 participants in the final sample (7 males; mean age 27), and experiment 2 (red, purple, blue, lime) included 14 participants in the final sample (7 males; mean age 25). Due to the difficulty of the task, one further participant in experiment 1 was excluded based on low performance in the training session (see Stimuli and Procedure section for more detail). All participants had normal or corrected-to-normal vision, and normal colour vision as assessed by the Cambridge Colour Test (Regan et al., 1994). Individual written informed consent was obtained, and the study was approved by the ethics committee of the School of Psychology, University of Aberdeen and found to be in accordance with the Declaration of Helsinki.

2.2 Stimuli and Procedure

We used RDKs with dots of four different chromaticities. Hues were defined based on normative unique hue data (Wuerger, 2013; Wuerger et al., 2005), yielding a set of colours that were qualitatively sufficiently different and could thus be discriminated from each other even when occupying the same spatial location. Red, blue, green and yellow are unique hues, and whereas all colours can be described in terms of these four hues, the unique hues

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themselves are not further reducible. We decided to use the unique hues based on a preliminary experiment, in which we found no difference between unique and intermediate hues (see Supplementary Material 1; our results are in line with Bosten and Boehm, 2014). Intermediate hues were calculated by interpolation based on unique hues. In the first experiment, which contained colours that were broadly and relatively evenly spread in perceptual colour space, we chose red, blue, green and yellow. In the second experiment, which contained colours that were unevenly spread in perceptual colour space, we chose red, purple, blue and lime. All hues were of equal chroma and lightness in CIE Lch space ($c=50$, $L=76$). The CIE 1931, CIE LUV and MacLeod-Boynton (MB) coordinates of the colours are presented in Table 1. The colours are represented in Figures 1 and 2a. The background was kept at a constant grey hue (CIE 1931 coordinates: $x=0.2843$, $y=0.2916$, $Y=23.36$ cd/m²; same as in the normative studies by Wuerger and colleagues) to ensure steady adaptation. The field occupied by the random dot stimuli extended over a circular area with a diameter of 12.32°. Each of the four colours was represented by 75 square-shaped dots of 0.31° of visual angle, which made 0.05° displacements per frame in a random direction. The dots were drawn in random order to prevent systematic overlap.

Table 1: Coordinates of Stimulus Colours in CIE LUV, MB and CIE 1931 colour spaces

| CIE LUV coordinates | | | |
|------------------------------------|---------|---------|---------|
| | L | U | V |
| Red | 76 | 48.50 | 12.17 |
| Blue | 76 | -26.72 | -42.26 |
| Purple | 76 | 29.31 | -40.51 |
| Lime | 76 | -12.32 | 48.46 |
| Yellow | 76 | 16.81 | 47.09 |
| Green | 76 | -37.27 | 33.33 |
| MacLeod-Boynton coordinates | | | |
| | L/(L+M) | M/(L+M) | S/(L+M) |
| Red | 0.67 | 0.33 | 1.16 |
| Blue | 0.60 | 0.40 | 2.10 |
| Purple | 0.65 | 0.35 | 1.98 |
| Lime | 0.63 | 0.37 | 0.79 |
| Yellow | 0.65 | 0.35 | 0.76 |
| Green | 0.60 | 0.40 | 1.02 |
| CIE 1931 coordinates | | | |
| | x | y | Y |
| Red | 0.3521 | 0.2966 | 49.89 |
| Blue | 0.2251 | 0.2439 | 49.89 |
| Purple | 0.2891 | 0.2339 | 49.89 |
| Lime | 0.3103 | 0.3795 | 49.89 |
| Yellow | 0.3481 | 0.3645 | 49.89 |
| Green | 0.2618 | 0.3612 | 49.89 |

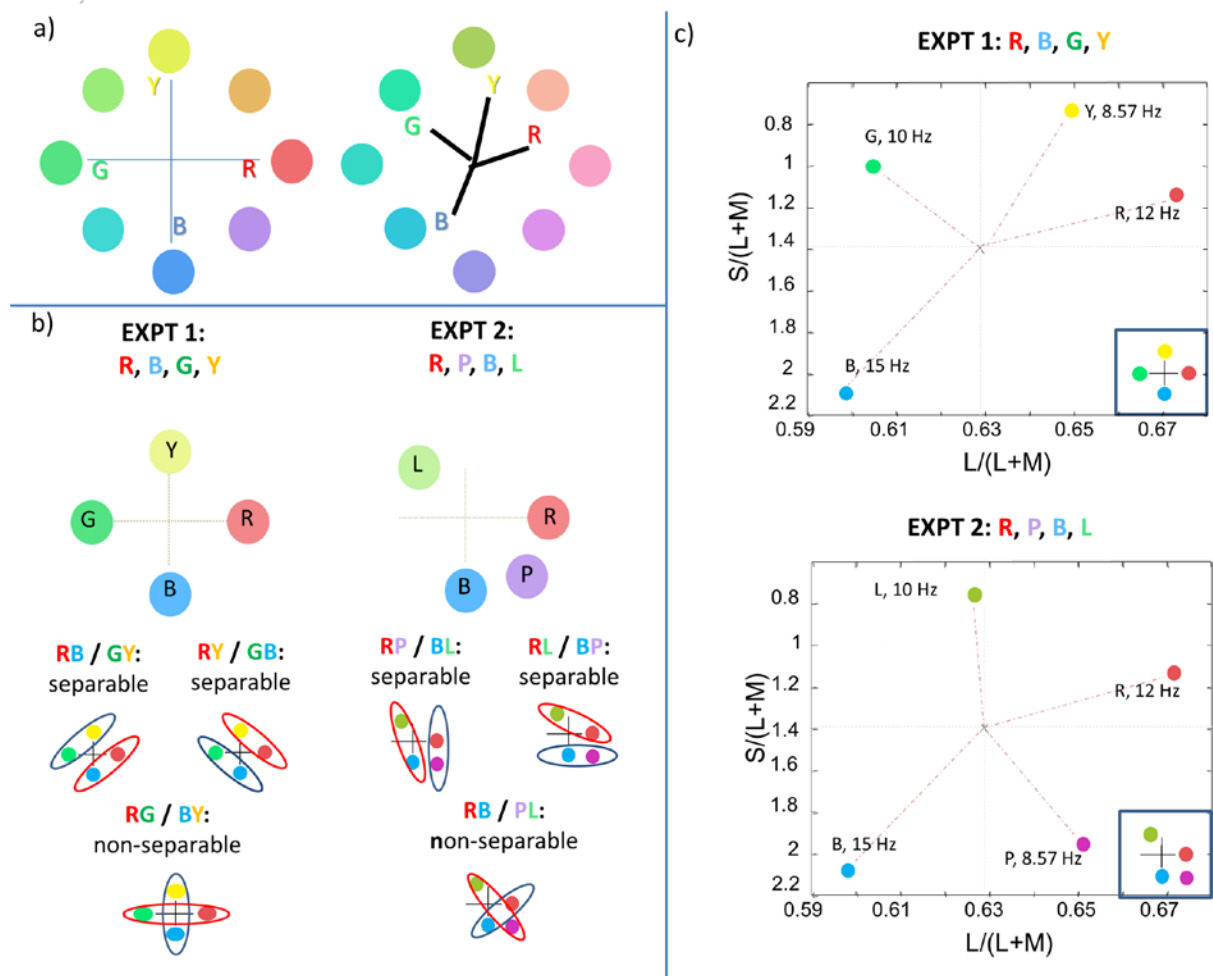


Figure 1. Colour spaces and stimulus colours. A) Colour spaces. On the left, a hue space is represented, defined by the colour-opponent axes red-green and blue-yellow; on the right, a cone-opponent space is represented, and in its centre are denoted relative positions of the unique hues that define the axes in the colour-opponent space (as per Wuerger, Atkinson and Cropper, 2005) to indicate that the two spaces do not map onto each other in a simple way. B) Stimuli used in our experiments are represented in the colour-opponent space, with the four unique hues (Red, Blue, Green and Yellow) from experiment 1 on the left hand side, and the four mixed hues (Red, Purple, Blue, Lime) from experiment 2 on the right hand side. Note that while the distances between the different hues in the colour-opponent space are

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approximately the same in experiment 1, they differ in experiment 2, with C2 (lime) being more distant from the other colours. The experimental conditions are shown below: participants attended two colours whilst ignoring the other two colours, giving three possible combinations of attended/unattended colours; two of these combinations required pairs of linearly separable colours to be attended and ignored (e.g., red & blue, green & yellow), and the third combination required pairs of linearly non-separable colours to be attended and ignored (e.g., red & green, blue & yellow). C) Stimuli used in our experiments are shown in MB space, which represents the excitations of the two cone-opponent chromatic mechanisms ($L/(L+M)$ and $S/(L+M)$) relative to the background (depicted with an 'X' in the middle of the diagrams). We defined the colours using a perceptual colour space. In the MB colour space, RPBL in experiment 2 are more evenly spaced than RBGY in experiment 1, as blue is further from the other colours in experiment 1. This differs from the spacing in hue-based space, where the colours in experiment 1 are more evenly spaced and the colours in experiment 2 are unevenly spaced.

As depicted in Figure 2, after viewing a fixation cross that lasted around 3 seconds, participants observed a cue for 600 ms on each trial. This cue instructed them to attend to two of the colours simultaneously and to detect brief coherent motion translations in either of these colours while ignoring such events in the other two colours. The cue was followed by 0.75-1 seconds of fixation prior to the interval of flickering dot stimulation, which lasted 3.14 seconds and could involve from zero to three coherent motion events embedded within random, independent dot motion. Coherent motion events could occur from 600 ms after trial

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onset onwards, lasted for 400 ms and involved 50% of the dots of one colour, randomly selected from each frame, moving in the same cardinal direction (up, down, left or right). The onsets of sequential coherent motion events were separated by at least 700 ms. Manual detection responses that occurred within 250-900 ms after the onset of coherent motion events in attended or unattended colour dot fields were counted as hits or false alarms, respectively. Similarly, events that did not receive a response in this period were counted as misses or correct rejections. Participants performed 600 trials, with 100 trials per condition; 70 of these trials contained no events, and the remaining 30 trials contained between 1 and 3 events. Thus, there were 180 target and 180 distractor events distributed through the trials (30 per condition each). Trials having different pairs of attended colours were presented in random order and split into 12 blocks of 50 trials each.

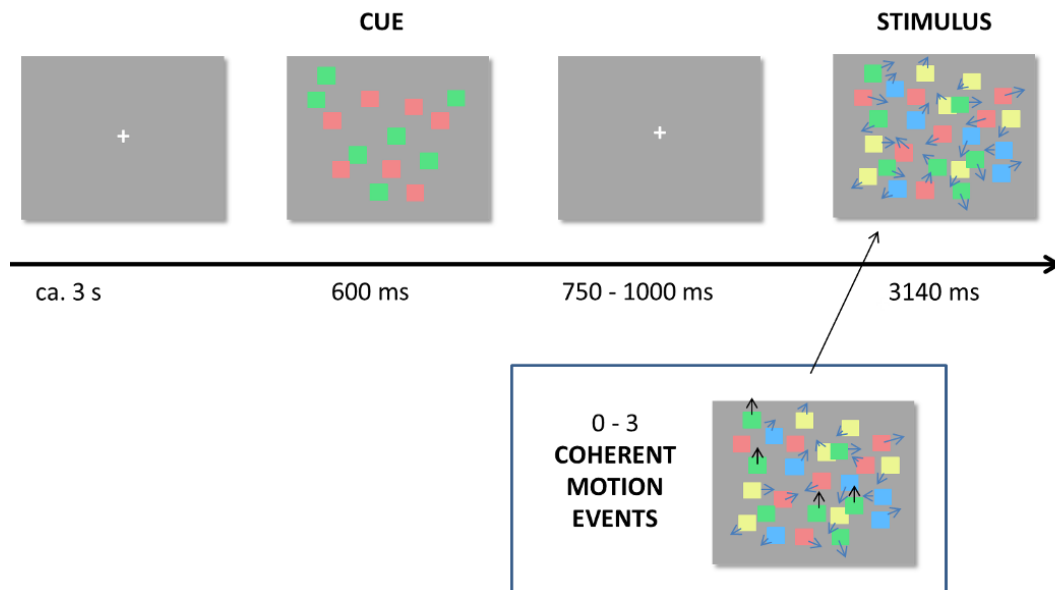


Figure 2. Overview of the experimental procedure. On each trial participants were cued to attend to two colours simultaneously and after a delay of 0.75-1.0 s observed a stimulus interval having the four flickering dot populations of different colours intermingled spatially

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and moving at random. Each stimulus interval could contain between 0 and 3 brief coherent movements of either of the the attended or the unattended dot populations. Participants responded with a button press to coherent motion in either of the attended colours while refraining from responding to the unattended colours. The number of dots is reduced for the sake of clarity; the colours from experiment 1 (RGBY) are used in this example.

The dots of each colour flickered at a specific frequency to tag the processing of each of the four colours independently. In experiment 1 (red, blue, green, yellow), yellow flickered at 8.57 Hz, green at 10 Hz, red at 12 Hz and blue at 15 Hz. In experiment 2 (red, purple, blue, lime), purple flickered at 8.57 Hz, lime at 10 Hz, red at 12 Hz and blue at 15 Hz. These frequencies correspond to flicker cycles of 14, 12, 10, and 8 frames, respectively, at a monitor refresh rate of 120 Hz. The on-off ratio for each frequency was 50-50; e.g., 10 Hz flicker was produced by presenting the dots for 6 frames and then switching them off for another 6 frames. The frequencies used here are within the range employed in our previous SSVEP-experiments with similar stimuli (e.g. Andersen et al., 2008, 2011, 2013, 2015; for a review, see Andersen et al., 2011b). Attention effects did not differ in a frequency-dependent fashion in those previous experiments, and therefore we did not counterbalance the assignment of frequencies to stimuli. Although such counterbalancing would be technically feasible, it comes with distinct disadvantages that we believe would outweigh any benefits. Especially, the need to average EEG epochs of each attention condition separately prior to collapsing across frequency assignments would exacerbate issues due to variability in the numbers of trials remaining after artefact correction and thereby negatively affect the precision of SSVEP

amplitude measurements. Participants initially completed a separate 45-minute training session with auditory feedback (low beep for a miss/false alarm, high beep for a hit), using a higher number of trials with target and distractor events to allow participants to familiarise themselves with the task. The training started with the divided attention task without flicker (which made the task considerably easier), and flicker was introduced once participants were comfortable with the task itself. On this basis, one participant was excluded, as described in the Participants section. The main experimental session lasted 3 hours, which incorporated 1-2 refresher practice blocks and an approximately 1 1/2 hour recording period.

The experiments were conducted using a DELL PC with a visual stimulus generator (VISaGe; CRS, UK). The stimuli were displayed on a 21" Viewsonic P227f CRT Monitor with a refresh rate of 120 Hz, calibrated with a ColorCAL 2 (CRS, UK) and controlled by the VISaGe system. CRS toolbox and CRS colour toolbox for Matlab (Mathworks, USA) were used to run the experiments. The CRS Colour Toolbox (CRS, UK; Westland et al., 2012) was used to generate the chromatic stimuli. This was based on measurements of the spectra of the monitor phosphors taken by a SpectroCAL (CRS, UK). Participants were seated in a dark room in front of the monitor, which was the only source of light. They gave their responses using a CT-6 button box (CRS, UK).

2.3 EEG data acquisition and analysis

Participants were seated in a comfortable chair in an electrically shielded chamber. Brain electrical activity was recorded at a sampling rate of 256 Hz from 64 Ag/AgCl electrodes mounted in an elastic cap using an ActiveTwo amplifier (BioSemi, Netherlands).

Lateral eye movements were monitored with a bipolar outer canthus montage (horizontal electro-oculogram). Vertical eye movements and blinks were monitored with a bipolar montage positioned below and above the left eye (vertical electrooculogram).

EEG data were processed using the EEGLab toolbox (Delorme and Makeig, 2004) in combination with custom-made procedures in Matlab. A period of 500 ms after stimulus onset was discarded to exclude the evoked response to stimulation onset and to allow the SSVEP sufficient time to build up. Further, from 2900 ms after stimulus onset, the data were also discarded, as in this period participants might become aware that no further events were possible, and this knowledge could have led participants' attention to diminish. This resulted in epochs of 2400 ms duration being extracted for SSVEP analysis. All epochs with target or distractor onsets occurring within the epoch were excluded from the SSVEP analysis. This ensured that the analyzed data were not contaminated by activity related to coherent motion or manual responses and left a total of 70 epochs for each condition. All epochs were detrended (removal of mean and linear trends). Epochs with eye movements or blinks were rejected from further analysis, and all remaining artifacts were corrected or rejected by means of an automated procedure (FASTER; Nolan et al., 2010). The average rejection rate was 12% in experiment 1 (red, blue, green, yellow) and 19% in experiment 2 (red, purple, blue, lime). While FASTER was conducted using Fz as reference, data were subsequently transformed to average reference. All epochs within the same condition were averaged for each participant. These means were Fourier-transformed, and SSVEP amplitudes were quantified as the absolute value of the complex Fourier-coefficients at the four stimulation frequencies. Based on the topographical distribution of mean SSVEP amplitudes a cluster of

5 electrodes (POz, Oz, O1, O2, Iz) where amplitudes were maximal was chosen and amplitudes were averaged across these electrodes for statistical analysis. SSVEP amplitudes usually exhibit considerable variability between frequencies and participants. We therefore normalised (rescaled) SSVEP amplitudes for each frequency (colour) and participant to a mean of 1.0 across all attentional conditions following the procedure described in Andersen, Fuchs and Müller (2011a). This facilitates comparisons of SSVEP amplitudes by equating the overall magnitude (but not the variance or distribution) between frequencies (colours). Attentional effects were then computed by subtracting rescaled amplitude when attended from rescaled amplitude when unattended (A-U). By normalising SSVEP amplitudes for each colour across different target/distractor pair conditions, it was possible to calculate unbiased attentional effects for each colour between conditions.

2.4 Statistical Analysis

For SSVEP analyses, there were two main factors in the experiments. The first was *colour*, with 4 colours. In experiment 1, these were red, blue, green and yellow and in experiment 2, these were red, purple, blue and lime. The second factor was *target/distractor configuration*, specifying the pairings of colours that were attended/ignored (e.g., attend red and yellow and ignore blue and green, and vice versa). Each colour could be attended in three combinations: either with a linearly non-separable colour or with one of the two linearly separable colours (see Figure 1). In experiment 1 (red, blue, green, yellow), red and blue were attended as a linearly separable pairing, while in experiment 2 (red, purple, blue, lime) they were attended as a linearly non-separable pairing. Therefore, the analysis of attentional effects in SSVEPs has the potential of not only informing us whether concurrent selection of

two colours is achieved at the neural sites indexed by the SSVEPs, but also in clarifying whether this effect depends on linear separability between targets and distractors, as well as establishing whether linear separability is confounded with colour distances by comparing attention effects obtained in the broad and relatively evenly spread colour context from the first experiment with the non-even colour context from the second experiment.

The analysis of hit rates, false alarms, criterion measures and RTs was somewhat different, as these measures were combined over the two distractor and two target colours. Therefore, we had the factor *attended colour pair*, with 6 levels, as that was the total number of possible combinations of target colour pairs. For RTs, we also did an additional analysis by colour, collapsing across target colour pairs.

We tested the significance of the attention effects using repeated measure ANOVAs. As outlined above, hit rates, false alarm rates, RTs and criteria were tested using single-factor ANOVAs. Attentional effects on the SSVEPs were tested using a 3 x 4 design with the factors of *target/distractor configuration* (*two linearly separable and one non-separable pairing*) and *colour*. Greenhouse-Geisser correction was used when necessary, and repeated measure ANOVAs and/or Bonferroni-Holm corrected paired t-tests were used for post-hoc testing. Cohen's d effect sizes were computed for paired t-tests, using Morris and DeShon's (2002) correction for dependence between means. Attentional effects were also tested against zero using a one-sample t-test.

3. Results

3.1 Experiment 1, red, blue, green and yellow

3.1.1. **Behavioural results:** Collapsed across all attentional conditions, means and standard errors were as follows: hit rate $61\% \pm 4\%$, false alarm rate $22\% \pm 3\%$, reaction times $584\text{ ms} \pm 16\text{ ms}$ and the criterion 0.25 ± 0.11 , indicating that the coherent motion detection task was difficult but achievable and that the participants had a somewhat conservative criterion. Both the difficulty of the task and the conservativeness in the response criterion are directly attributable to the addition of flicker, as our preliminary behavioural experiment with the same hues but without flicker found much better performance joined with a somewhat liberal response criterion (Supplementary Material 1).

Behavioural results are depicted in Figure 3a, with hits and false alarms depicted in the top row, criterions in the middle row and reaction times in the bottom row. For each of these dependent variables, we tested whether there were differences in performance when attending to different target pairs. A repeated measures ANOVA on hit rate data did not show an effect of *attended colour pair* ($F(5, 55) = 1.55, p = .19$). However, differences between *attended colour pairs* were present in false alarm rates ($F(5, 55) = 8.68, p < .001, \eta_p^2 = .44$). The post-hoc paired t-tests showed a significantly higher false alarm rate for green/red compared to blue/yellow ($t(11) = 6.94, p < .001, d = 2.30$), blue/green ($t(11) = 4.90, p < .001, d = 1.65$) and red/yellow ($t(11) = 3.69, p = .0035, d = 1.07$). A repeated measures ANOVA on criterion data showed a significant effect of *attended colour pair* ($F(5, 55) = 3.77, p = .005, \eta_p^2 = .26$). Post-hoc paired t-tests indicated a less conservative criterion for green/red

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compared to blue/yellow ($t(11) = 5.38, p < 0.001, d = 1.54$). No differences in RTs were found (by attended colour pair: $F(5, 55) = 1.11, p = .37$; by colour: $F(3, 33) = 2.07, p = .12$).

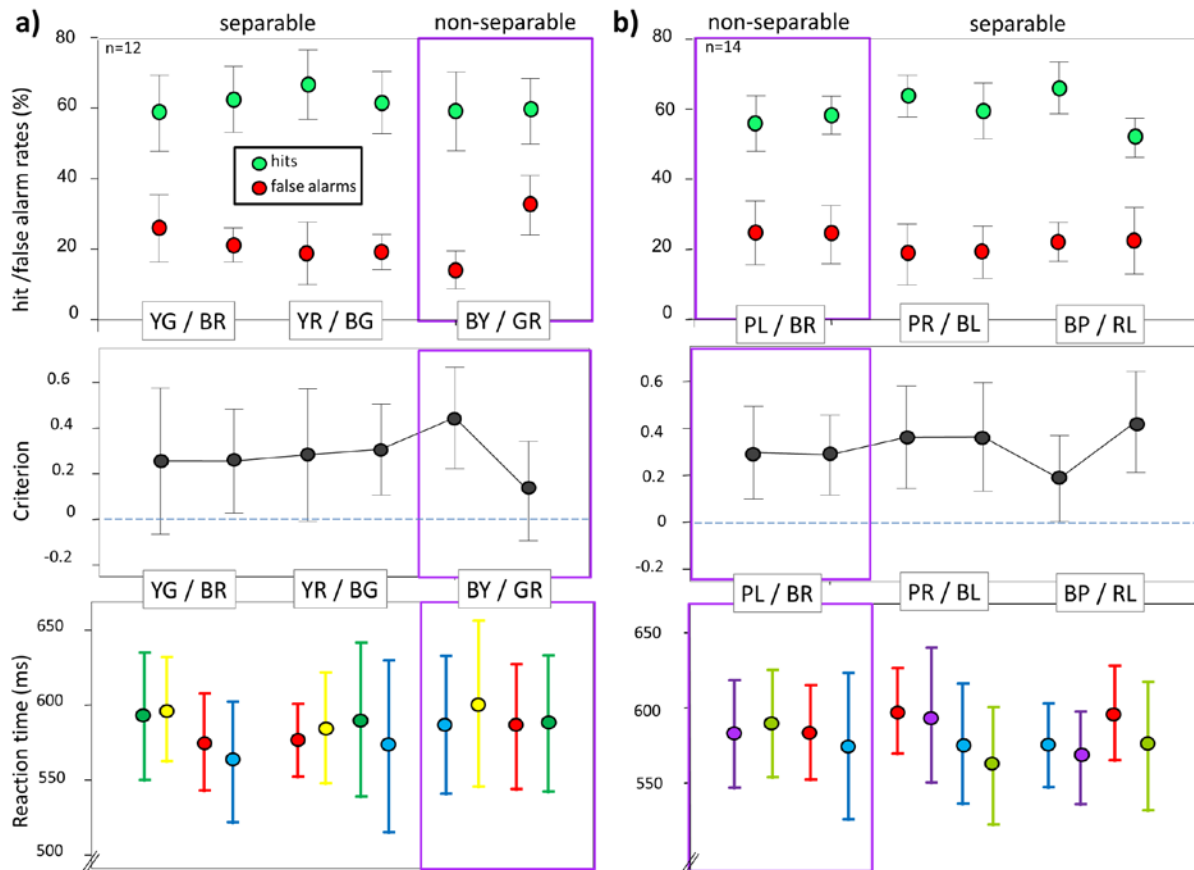


Figure 3. Behavioural performance: means of hits and false alarm rates, reaction times and criteria. A) Experiment 1: Red, Blue, Green and Yellow (R, B, G, Y). B) Experiment 2: Red, Purple, Blue and Lime (RPBL). Conditions are denoted both by referring to the combinations of targets/distractors using colour initials (e.g., GY / RB for green & yellow/red & blue) and by an image showing the set of 4 colours positioned in hue space for each combination, as depicted previously in Figure 1b, with attended colour pairs enclosed in ovals. Error bars depict 95% CIs.

3.1.2 SSVEP results: Figure 4 (upper panel) depicts the amplitude spectra and topographies, showing that maximal activity was observed at occipital sites (POz, Oz, Iz, O1, O2) and that peaks in the spectra were robust at all four flicker frequencies. The top row of Figure 5a depicts the attentional effects for this experiment, derived by subtracting the normalised SSVEP amplitude when a colour pairing was attended (A) versus unattended (U). Collapsed across conditions the overall attentional effect ($A - U$) was significantly above zero ($M = 0.103$, $SE = 0.032$, $t(11) = 3.19$, $p = .009$), indicating that SSVEP amplitudes were enhanced by attention.

To determine whether linear separability influenced the concurrent selection of two colours, we conducted a repeated measures ANOVA of SSVEP attention effects with the two factors *target/distractor configuration* and *color*. The factor of *target/distractor configuration* was highly significant ($F(2, 22) = 17.15$, $p < .001$, $\eta_p^2 = .61$), with post-hoc t-tests revealing that this was caused by a reduced attentional effect for the non-separable green/red and blue/yellow pairings with respect to both separable pairings: yellow/green and red/blue ($t(11) = 4.40$, $p = .001$, $d = 1.28$) and red/yellow and blue/green ($t(11) = 4.98$, $p < .001$, $d = 1.63$). The attention effects of the latter two separable colour pairs did not differ significantly from each other ($t(11) = 1.57$, $p = .14$). There were also significant differences between *colours* ($F(3, 33) = 3.49$, $p = .027$, $\eta_p^2 = .24$), with attentional effects for yellow tending to be higher overall than for blue ($t(11) = 2.92$, $p = .014$, critical p value reduced to $p = .008$ due to multiple comparisons). No interaction between the two factors was observed ($F(3.37, 37.08) = 1.91$, $p = .139$).

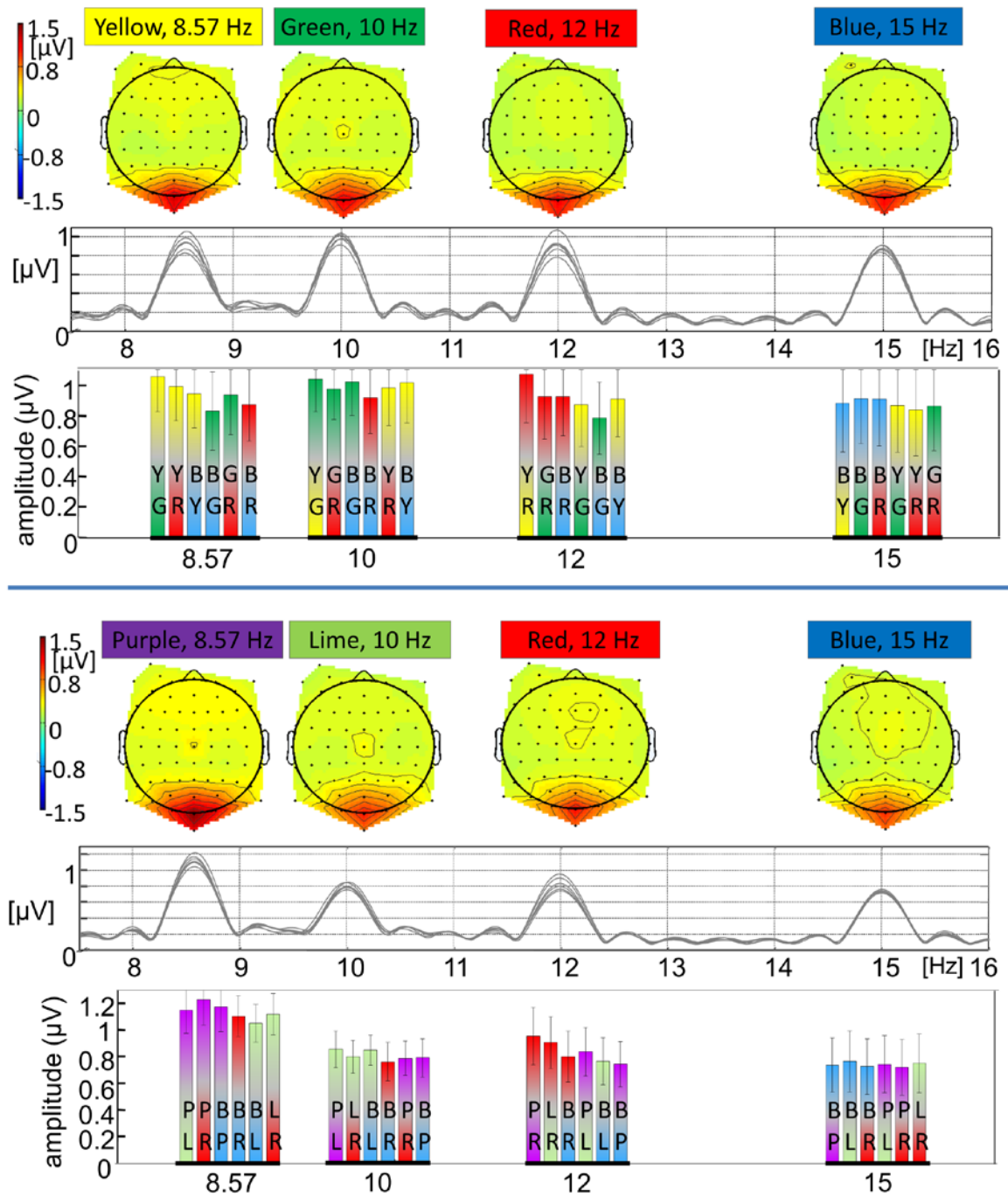


Figure 4. SSVEPs in experiment 1 (red, blue, green, yellow; upper panel) and experiment 2 (red, purple, blue, lime; lower panel). Topographies of SSVEPs, collapsed across all conditions, indicate a maximum amplitude over occipital scalp (POz, Oz, Iz, O1, O2). EEG

activity at these electrodes is depicted in the graph of the spectra beneath, accompanied by a bar chart of raw SSVEP amplitudes with 95% CIs. Different combinations of colours are labelled with the same abbreviations as in previous figures: Y for yellow, G for green, R for red and B for blue, P for purple, L for lime.

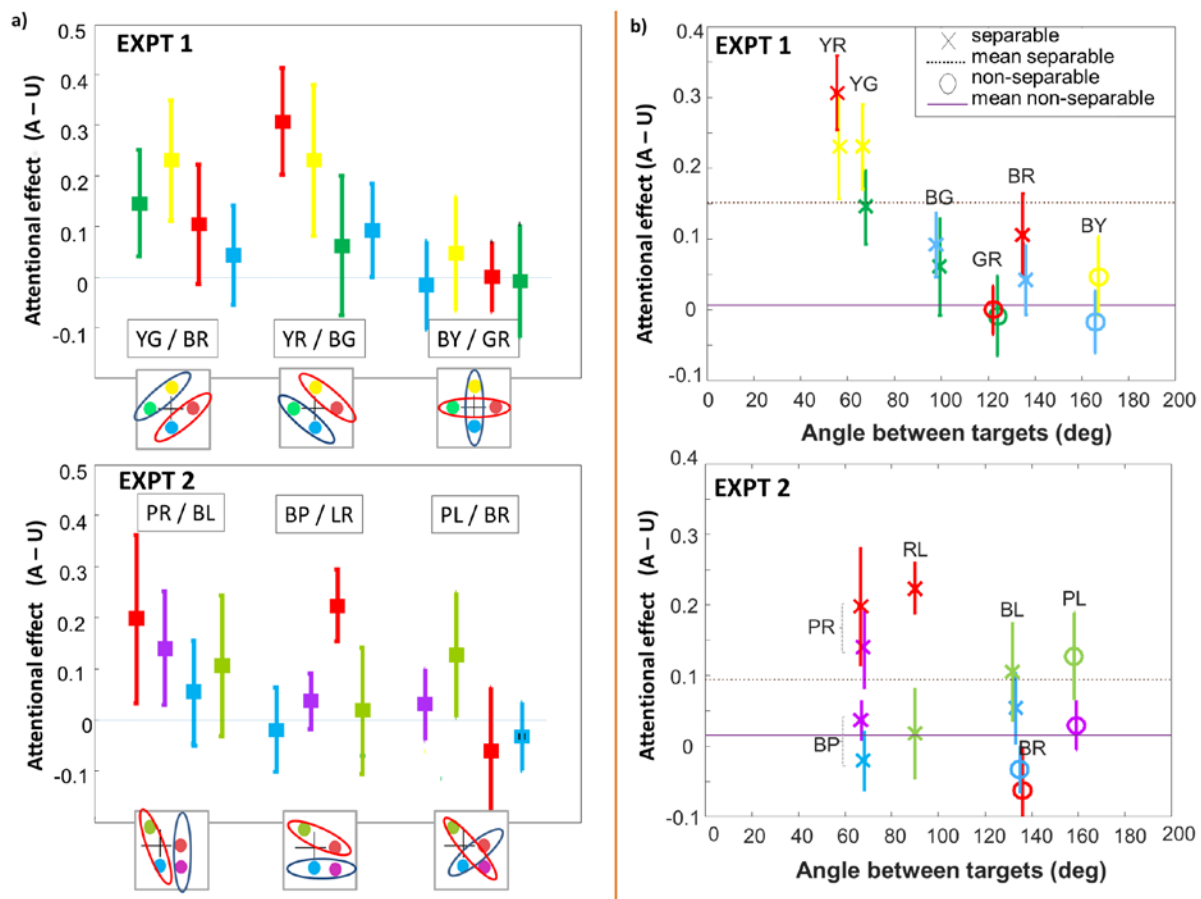


Figure 5. Attentional effects on SSVEPs. a) Plots of grand-mean attentional effects computed from normalised SSVEP amplitudes for both experiments. The attentional effects represent the increase in SSVEP amplitude for an attended colour (A) relative to that same colour when unattended (U) within each pairing of targets and distractors. Colour abbreviations as in previous figures (R for red, B for blue, G for green, Y for yellow, P for purple and L for lime). The error bars show 95% confidence intervals. It can be seen that

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when linearly non-separable combinations of colours are attended, there is no reliable increase in SSVEP amplitude elicited by the attended colours. b) Attentional effects on SSVEPs are plotted as a function of distance between the targets. Colour distances are quantified in terms of angles between the two targets in CIE LUV space. The average across all linearly separable targets (crosses) is shown by the dotted line, while the average across all non-separable targets (circles) is shown by the full line. For each pair, the attended colours are indicated by initial letters, e.g. RY for red/yellow. Error bars represent 1 standard deviation.

3.1.3 Interim discussion

The results of experiment 1 confirm that concurrently attending two colours enhances their SSVEP amplitudes and that this effect may also depend upon the linear separability of targets from distractors. However, due to the relatively even spread of the four colours in perceptual colour space, this interpretation is ambiguous because the two target colours were also more widely separated in the non-separable conditions (see Figure 1). Therefore, we conducted a second experiment with a set of non-evenly distributed colours using the same experimental protocol, which allows us to disentangle linear separability and target proximity. In this experiment, the goal was first, to replicate the findings of experiment 1 on divided attention to colour in a different colour context, and second, to extend them by obtaining data that allow a direct comparison between linear separability and target proximity.

3.2 Experiment 2, red, purple, blue and lime

3.2.1. **Behavioural results:** Collapsed across all conditions, hit rates were $59\% \pm 2\%$, false alarm rates were $22\% \pm 3\%$, RTs were $581\text{ ms} \pm 14\text{ ms}$, and the criterion was 0.31 ± 0.08 . This was a very similar level of performance to that observed in experiment 1 (red, blue, green, yellow) and again confirms that the task was challenging but achievable and that most participants adopted a relatively conservative criterion.

Behavioural data are depicted in Figure 3b, with hits and false alarms in the top row, criteria in the middle row and RTs in the bottom row. A repeated measures ANOVA of the hit rates showed a significant difference between *attended colour pairs* ($F(5, 65) = 3.89$, $p = .004$, $\eta_p^2 = .23$). This was due to the fact that hit rates were higher for attending purple/blue than lime/red ($t(13) = 4.25$, $p = 0.001$, $d = 1.16$). Although both of these pairs were linearly separable, target proximity was closer for purple/blue than lime/red. No significant differences in false alarm rates were found ($F(5, 65) = 1.43$, $p = .23$). A repeated measures ANOVA of the criterion also showed an effect of *attended colour pair* ($F(5, 65) = 2.76$, $p = .025$, $\eta_p^2 = .18$). Post-hoc tests were inconclusive, due to the criterion p value being reduced to $p = .0033$ to account for 15 comparisons, although there was a strong trend for a less conservative bias for purple/blue compared to red/yellow ($t(13) = 3.36$, $p = .0051$, $d = 0.92$).

No RT differences were found between attended colour pairs ($F(5, 65) = 0.52$, $p = .76$) or colours ($F(3,39) = 1.45$, $p = .24$).

3.2.2. **SSVEP results:** Figure 4 depicts the amplitude spectra and topographies, showing that maximal activity was observed at occipital sites (POz, Oz, Iz, O1, O2) and that peaks in the spectra were robust at all four flicker frequencies. The bottom row of Figure 5a

depicts the attentional effects derived by calculating the difference in normalised SSVEP amplitudes when a colour pair was attended (A) versus unattended (U). Collapsed across conditions the overall attentional effect was significantly above zero ($M = 0.068$, $SE = 0.019$, $t(13) = 3.53$, $p = .004$), confirming that concurrent selection of two colours enhanced their SSVEP amplitudes.

To determine whether linear separability influenced such concurrent selection of colour, we conducted a repeated measures ANOVA on SSVEP amplitudes. There was a significant difference between attentional effects (A – U) according to *attended colour pair* ($F(2, 26) = 4.92$, $p = .015$, $\eta_p^2 = .28$), driven by a tendency towards a lower effect for the non-separable purple/lime and red/blue pairing than for the separable purple/red and blue/lime pairing ($t(13) = 2.69$, $p = .019$; Bonferroni-corrected criterion being $p = .017$). There were no significant differences as a function of *colour* ($F(1.69, 21.92) = 1.43$, $p = .26$). However, this time there was a significant interaction between the two factors ($F(6, 78) = 3.53$, $p = .004$, $\eta_p^2 = .21$). This interaction was decomposed for each colour using four repeated measures ANOVAs with the factor *attended colour pair*, reducing the p value from .05 to $p = .0125$. The interaction was driven by differences for red ($F(2, 26) = 7.19$, $p = .003$, $\eta_p^2 = .36$), with post-hoc t-tests revealing that the attentional effect (A -U) for red when attended with blue (non-separable) was lower than for red/purple ($t(13) = 4.03$, $p = .001$, $d = 1.11$) and red/lime ($t(13) = 3.42$, $p = .005$, $d = 0.94$). The ANOVAs for the other colours were not significant (purple: $F(2, 26) = 2.63$, $p = .09$; lime: $F(2, 26) = 1.99$, $p = .16$; blue: $F(2, 26) = 1.01$, $p = .38$).

3.3 Contrasting the attentional effects of target similarity and linear separability

Linear separability is necessarily confounded with target-target and target-distractor distances, especially in an experiment such as ours that needs to utilise colours that can be easily distinguished when presented together. Indeed, inspection of Figure 5b reveals that the angle between any two colours was never below 50° in CIE LUV space.

Still, it is possible to directly contrast the relative contributions of linear separability and colour similarity using the present data. Unlike the first experiment, which used four hues that belonged to the axes of the perceptual colour space and were thus relatively broadly spread in perceptual colour space, the second experiment combined two unique hues (red and blue) with two intermediate hues, one of which was relatively close to them (purple) and one of which was relatively far from them (lime) in perceptual colour space. This configuration enables us to contrast the contribution of linear separability and target proximity, as these factors would predict different attentional effects for certain colours. If colour proximity were the only influence on attention even when multiple targets are to be selected concurrently, then attentional increase in SSVEPs for red and blue when attended together should be higher than for red or blue when attended with lime. On the other hand, linear separability would predict that attentional increase should be absent when attending red and blue together, as the purple and lime distractors would make them linearly non-separable. We averaged the attentional SSVEP effect for red and blue when either of them was attended with lime ($M = 0.14$, $SD = 0.11$) and for red and blue when attended with each other ($M = -0.05$, $SD = 0.13$) and found that the data were in line with the prediction based on linear separability ($t(13) = 3.81$, $p = .002$; $d = 1.02$). Indeed, when attended together, attentional SSVEP effects for

neither red ($t(13) = 0.95, p = .36$) nor blue ($t(13) = 0.93, p = .37$) were significantly different from zero.

As red and blue were used in both experiments, it is also possible to contrast their attentional SSVEP effects between subjects. Colour proximity remains constant across the two experiments, but in experiment 1 (red, blue, green, yellow), red and blue targets were not accompanied by non-separable distractors. An independent sample t-test revealed that the average attention effect (A-U) was greater for red and blue in experiment 1, in which the two colours were linearly separable, compared to experiment 2, in which they were not linearly separable from the distractors ($M = 0.075, SD = 0.16; t(24) = 2.11, p = .046, d = 0.83$).

3.4 Predicting Attentional Enhancement in SSVEP magnitude from distances in colour space

Both experiments clearly demonstrated that it is possible to divide early attentional resources across a non-spatial feature dimension, with linear separability in colour space being a determinant of such concurrent attention to two targets. On average, when targets and distractors were linearly separable, attentional enhancement was greater compared to the non-separable conditions (Fig. 6). However, there were also notable differences in attentional SSVEP effects between the two experiments, as well as between different colours. As depicted by Figure 5b, these differences cannot be accounted for simply by the different distances between various target colour pairs: while this seems to be a reasonable predictor of attentional effects in experiment 1 (red, blue, green, yellow), this was not the case for experiment 2 (red, purple, blue, lime). To gain a better understanding of these colour-related

attentional differences, we fitted a simple descriptive model to the attentional effects derived from the SSVEP data, making several basic assumptions. We hypothesized that attentional enhancement should be inversely related to the distance between the targets (Nagy and Thomas, 2003), that attentional enhancement should increase with the distance between a target and the mean distractors, and that these two factors should contribute to attentional enhancement independently. For example, the attentional enhancement for attending to red when it was attended together with green should be inversely related to the distance between the two targets (red and green) and linearly related to the distance between red and the mean of the two distractors (yellow and blue).

In these experiments observers were asked to attend to two colours (target colours: T_1 , T_2) in the presence of two distractors (distractor colours: D_1 , D_2). To elucidate how attentional enhancement depends on colour similarities of the four stimuli we make several assumptions:

Assumption 1: Attentional enhancement for target colour T_1 is inversely proportional to the dissimilarity (d) between the two targets; i.e. if the target colours are very similar to each other, we assume that it is easier to simultaneously attend to these colours:

$$a_{T_1 D_{12}} \sim \frac{1}{d(T_1, T_2)} \quad (1)$$

Assumption 2: Attentional enhancement is proportional to the dissimilarity between the target colour and the mean distractor colour; i.e., if the dissimilarity between the target (T_1) and the

average distractor colour ($D_{1,2}$) is large, it should be easier to attend to the target colours and ignore the distractors.

$$a_{T_1 D_{1,2}} \sim d(T_1, D_{1,2}) \quad (2)$$

Assumption 3: We assume that these two components contribute to the attentional enhancement independently which allows us to formulate a simple model:

$$a_{T_1 D_{1,2}} = w_{TT} \frac{1}{d(T_1, T_2)} + w_{TD} d(T_1, D_{1,2}) \quad (3)$$

a_T is the attentional modulation for target colour T_1 with distractor combination D_1 and D_2 , w_{TT} is the weight parameter for target proximity and w_{TD} the weight factor for the dissimilarity between target and mean distractor. These two parameters will be estimated from the data.

Assumption 4. The dissimilarity between two colours can be described as the Minkowski distance between these two colours, with p being the summation coefficient to be estimated from the data.

$$d(C_1, C_2) = \left[\sum_{i=1}^2 (C_{1i} - C_{2i})^p \right]^{\frac{1}{p}} \quad (4)$$

For $p=2$, the Minkowski metric is simply the Euclidean distance, $p=1$ corresponds to linear summation and $p \rightarrow \infty$ reflects a maximum rule. Since all colours were of approximately the same luminance, distances are only computed in the two-dimensional chromatic plane of the

cone-opponent space where the axes represent the $L/(L+M)$ and $S/(L+M)$ direction, respectively.

Assumption 5. Since the relative scaling of the cone-opponent axes is arbitrary, a scaling factor (s) for the $S/(L+M)$ axis is required which reflects the relative weighting of the two cone-opponent mechanisms. The scaling factor for $L/(L+M)$ is set to 1. The scaling factor for the $S/(L+M)$ axis is a free parameter and estimated from the data.

Choice of Colour space. We perform the fits and present the results in cone-opponent MB space as it allows the interpretation of the estimated parameters in terms of neural chromatic mechanisms. To ensure that our results are robust and not contingent on the particular choice of colour space, the stimuli for both experiments are presented in both the cone-opponent MB space and CIELUV colour space. Figure 6 shows that the cone-opponent axes can be scaled such that the relative loci of the stimuli and the relative distances between the stimuli are very similar.

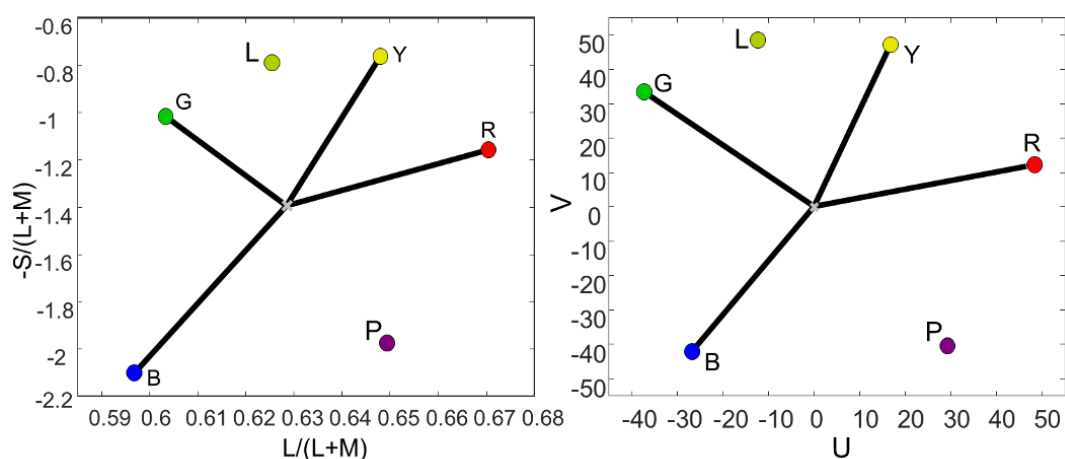


Figure 6. Stimuli plotted in a cone-opponent MB space (left) and in a uniform CIELUV space (right). Unique hues are connected by black lines which originate from the neutral

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locus (background colour; grey cross). Loci and angles between stimuli are very similar in both representations. R: Red, G: Green, B: Blue, Y: Yellow, L: Lime, P: Purple.

Model fits. Equation 3 defines the model that was fitted to the attentional effects (A – U) derived from normalised SSVEP amplitudes. The attentional enhancement (in terms of change in SSVEPs) for a particular target colour (T_1), presented together with target colour T_2 , in the presence of distractors (D_1, D_2), is predicted by the similarity between the target colours and the distance of the target colours from the mean distractor colour. In the most general model (Model 3a), four free parameters are estimated from the data (see Table 2): the scale factor s , weighting factor for target similarity w_{TT} , the weighting factor for dissimilarity between target and distractors w_{TD} and the Minkowski summation coefficient.

Table 2. Model (Mod), No of free parameters (No), parameter estimates and the resulting errors for the model, the coefficient of determination r^2 , and the goodness of fit.

| Mod | No | Parameter Estimates | | | | | | | AIC Weight |
|--|----|---------------------|--------------|--------------------------------|-------------|--------------|--------------|--------------|---------------|
| | | s | W_{TT} | W_{TD} | p | RSS | r^2 | ΔAIC | |
| EXPERIMENT 1 (RED, BLUE, GREEN, YELLOW) | | | | | | | | | |
| 1 | 2 | 0.060 | 0.011 | =0 | =2 | 0.039 | 0.749 | 4.11 | 0.0581 |
| | | 0.077 | 0.011 | =0 | =200 | 0.034 | 0.769 | 2.53 | 0.1282 |
| 2 | 3 | 0.077 | 0.011 | =0 | 213.7 | 0.034 | 0.770 | 6.17 | 0.0209 |
| | 2 | 0.054 | =0 | 0.120 | =2 | 0.194 | 0.053 | 23.18 | 0.0000 |
| 3a | 3 | 0.076 | =0 | 0.699 | =200 | 0.214 | 0.032 | 24.32 | 0.0000 |
| | | 0.076 | =0 | 0.011 | 179.9 | 0.214 | 0.032 | 27.99 | 0.0000 |
| 3b | 3 | 0.060 | 0.014 | 0.763 | =2 | 0.033 | 0.748 | 5.80 | 0.0251 |
| | | 0.074 | 0.012 | 0.845 | =200 | 0.028 | 0.781 | 3.66 | 0.0732 |
| 3b | 2 | 0.074 | 0.011 | 0.836 | 198.2 | 0.028 | 0.781 | 8.37 | 0.0069 |
| | | 0.061 | 0.018 | =1- w_{TT} | =2 | 0.033 | 0.748 | 2.13 | 0.1573 |
| 3b | 3 | 0.074 | 0.014 | =1- w_{TT} | =200 | 0.028 | 0.781 | 0 | 0.4562 |
| | | 0.074 | 0.014 | =1- w_{TT} | 199.4 | 0.028 | 0.781 | 3.66 | 0.0732 |
| EXPERIMENT 2 (RED, PURPLE, BLUE, LIME) | | | | | | | | | |
| 1 | 2 | 0.032 | 0.011 | =0 | =2 | 0.044 | 0.566 | 1.35 | 0.1687 |
| | | 0.039 | 0.011 | =0 | =200 | 0.046 | 0.554 | 1.86 | 0.1307 |
| 2 | 3 | 0.035 | 0.011 | =0 | 2.69 | 0.0439 | 0.568 | 5.53 | 0.0209 |
| | | 0.026 | =0 | 0.011 | =2 | 0.148 | 0.053 | 15.73 | 0.0001 |
| 3a | 3 | 0.029 | =0 | 0.110 | =200 | 0.171 | 0.017 | 17.45 | 0.0001 |
| | | 0.033 | =0 | 0.011 | 78.12 | 0.138 | 0.043 | 18.55 | 0.0000 |
| 3b | 2 | 0.030 | 0.013 | 1.205 | =2 | 0.039 | 0.584 | 1.67 | 0.1437 |
| | | 0.038 | 0.020 | 0.863 | =200 | 0.045 | 0.559 | 5.20 | 0.0246 |
| 3b | 3 | 0.029 | 0.011 | 1.059 | 1.79 | 0.039 | 0.585 | 10.0 | 0.0022 |
| | | 0.030 | 0.011 | =1- w_{TT} | =2 | 0.039 | 0.585 | 0 | 0.3313 |
| 3b | 3 | 0.038 | 0.023 | =1- w_{TT} | =200 | 0.045 | 0.559 | 1.53 | 0.1542 |
| | | 0.028 | 0.010 | =1- w_{TT} | 1.79 | 0.039 | 0.585 | 5.29 | 0.0235 |

To find the best-fitting parameter values, the mean square error between the SSVEP-derived attentional effects and the predicted attentional enhancement (Eq 3) is calculated for each observer. The objective function minimises the overall mean square error (over all subjects) using unconstrained nonlinear minimization (Nelder-Mead; function 'fminsearch', Matlab®). To evaluate the goodness of the fit, 95% confidence intervals were bootstrapped (function 'bootci', Matlab®; number of samples: 10000).

Model evaluation. To evaluate the relative importance of the model components (Eq. 3), nested models were tested. Model 1 is based on Eq. 1 and only includes target proximity, that is, w_{TD} is set to zero. Model 2 is based on Eq. 2 and only includes target-distractor distance, that is, w_{TT} is set to zero. Models 3a and 3b are the full model based on Eq. 3 and include both factors. In the most general model (model 3a), both weight factors, w_{TT} and w_{TD} , were free parameters, in addition to the scaling factor (s) and the summation coefficient (p). The goodness of the model fit is reflected in the residual errors (RSS, table 2) and the Akaike Information Criterion (AIC; Burnham and Anderson, 2002) with the latter taking into the account the number of free parameters. ΔAIC (2nd last column) indicates the difference in AIC value between each of the candidate models and the best model. The AIC weight (last column) is the likelihood for a particular candidate model to be the best model amongst all models considered for a given data set. In both experiments, the best model is Model 3b (ΔAIC is by definition 0 for the best model).

Initially, all models were fit with p as a free parameter. Since the data did not sufficiently constrain the value of p , it was subsequently fixed to $p = 2$ (i.e. Euclidean distance in colour space; row 1 within each model) or $p=200$ (converging to maximum rule;

row 2 within each model). When p was estimated (row 3 within each model), the residual error (RSS) did not decrease, but the AIC value is larger since an additional parameter is fitted. For Experiment 1, the best model is Model 3b with p fixed at 200 (Δ AIC is by definition 0 for the best model); for Experiment 2, the best model is also Model 3b with p fixed at 2.

Model 2 which assumes that attentional enhancement is accounted for solely by the distance between target and distractors can be excluded since the Δ AICs are well above 20 (for experiment 1) and above 10 (for experiment 2); models with Δ AICs above 10 are considered as unlikely in comparison to the best model (Burnham and Anderson, 2002).

Model 1 which only takes into account the target proximity has substantial support, in particular for experiment 2 with Δ AICs below 2. For experiment 1, there is less support for the model with Δ AICs between 2 and 4 (Burnham and Anderson, 2002), but no grounds to dismiss this model. In terms of evidence ratio (ratios between AIC weights, last column in Table 2), Model 3b is 3.3 times more likely than Model 1 for experiment 1, and only 1.5 times more likely for experiment 2. Hence, Model 1 should not be dismissed based on the AIC criterion.

In comparison, Model 1 (target proximity only) is 3000 times (experiment 1) and 1500 times (experiment 2) more likely than Model 2 (target-distractor distance only) hence Model 2 can clearly be dismissed. Similarly, there is no evidence for all model variations that estimate the summation coefficient p (row 3 within each model) since the Δ AICs are invariably larger when the coefficient is estimated.

Finally, when Model 3a (w_{TD} is estimated) and Model 3b ($w_{TD} = 1 - w_{TT}$) were fitted, it turned out that the data did not constrain the absolute values of these parameters and the RSS did not change when w_{TD} was set to $1 - w_{TT}$ (cf Table 2, rows 3 and 4 for both experiments). The evidence ratios (relative AIC weights) show that Model 3b is 6.5 (experiment 1) and 3 (experiment 2) times more likely than Model 3a.

In terms of residual error (RSS), Model 1 (Eq. 1) only includes target proximity, while model 2 (Eq. 2) only includes target-distractor distance. The error of model 1 is only slightly larger (10-20%) than model 3 which suggests that the distance between target and distractors is not a crucial factor for guiding attention in our experiments (cf. Table 2, error column between Model 1 and Model 3). In contrast, the error increases by a factor of 4-9 when only the distance between target and distractor is used to predict the attentional enhancement (cf Table 2; error column between Model 2 and 3).

It is clear from the figures below and the AIC analysis that the basic pattern of the attentional enhancement is fairly well predicted by Model 1 (target proximity only) and 3 (target proximity and target-distractor distance), but that Model 2 (target-distractor distance only) fails completely.

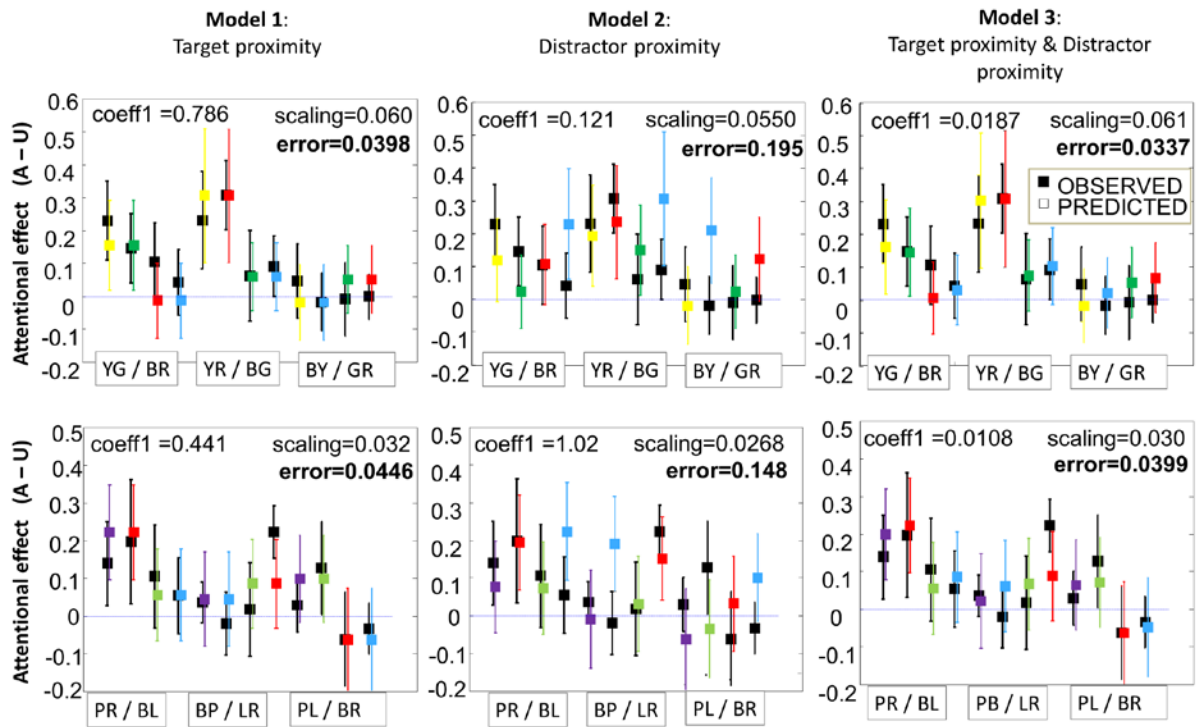


Figure 7. Model fits based on colour distances. Attentional effects obtained in the experiments (black squares and 95% CIs, as in Figure 6) are presented together with fitting outcomes (coloured squares with bootstrapped 95% CIs) based on our simple model whose aim was to explain relatively unexpected differences both between different colours and between the same colour in different combinations. The model accounts for attentional effects in neural activity as being due to the proximity of the second target and the distance to the mean distractor. Model 1 includes only target proximity, model 2 includes only distractor proximity, while model 3 includes both target proximity and target-distractor proximity. Very good fits were achieved for models that include target proximity (models 1 and 3), in all but 1 case within the 95% confidence interval. . The goodness-of-fit for model 1 (using only target

proximity) is almost as good as for model 3, which has an additional parameter and takes into account proximity to the distractor (cf Table 2).

These analyses indicate that the attentional effects on SSVEPs were best accounted for by target-target distances, with target-distractor distances playing only a small role. At first glance this may seem surprising, since target-distractor differences are essential for attentional selection. If targets and distractors are indistinguishable, selection is impossible. However, it is important to keep in mind that the conditions in the present experiments were designed to test divided attention to colour using displays with overlapping coloured dots that needed to be easily distinguishable from each other. Therefore, the lack of a more pronounced influence of target-distractor distance on attentional selection was likely a result of the specific conditions that were investigated. It should be kept in mind that while the present model is well-suited to explain the magnitude of attentional effects in our two experiments, the range of conditions investigated here is insufficient to produce a model of general validity across all arrangements of target and distractor colours.

Interestingly, the scaling factor turned out to be robust and did not change significantly with the different models. Both models that account for the data well (Model 1 and 3) result in similar scaling factors (s) for the S/(L+M) directions (cf Table 2). The ratio of the scaling factor between experiments is approximately 2:1, suggesting that the S cone input needs to be scaled twice as much in experiment 1 (red, blue, green, yellow) compared to experiment 2 (red, purple, blue, lime). The most parsimonious explanation is that these scaling factors change as a function of the set of target and distractor colours, since the task was identical in

both experiments. An intriguing speculation of this stimulus-set-dependent weighting, reflected in the different scaling factor, is that the visual system may adjust its weight such that the lines connecting the stimuli are orthogonalised, and thereby maximize the pairwise distances between the colour pairs. Figure 8 plots the colours within the cone-opponent MB colour space scaled in a way that predicts the SSVEPs. It can be observed that linearly non-separable colours indeed seem to be 'de-correlated', with angles between them approximately orthogonal. This prediction from our model is thought-provoking and should be tested in future by dedicated experiments.

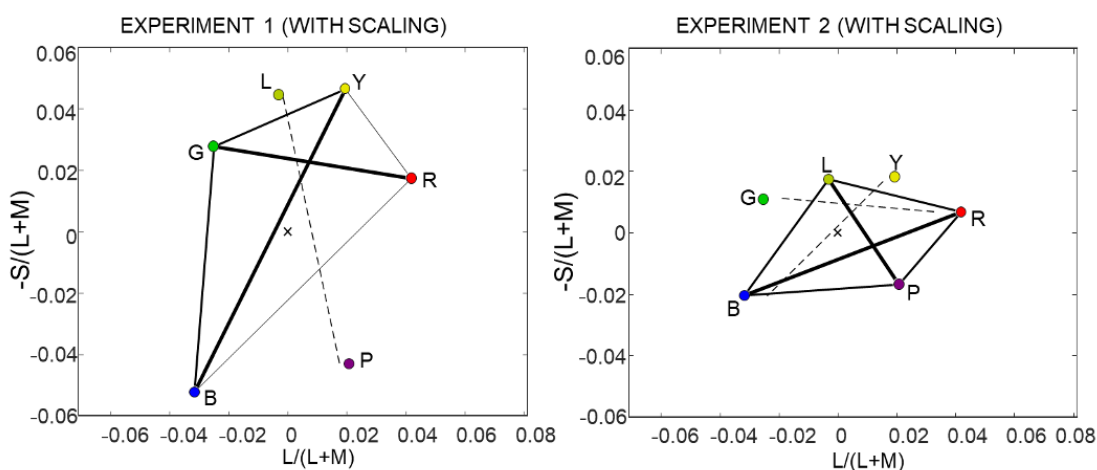


Figure 8. *Estimated scaling factors applied to the chromatic axes in both experiments. The relative scaling factor estimated from our full model is applied to the stimuli in MB space. Note that lines connecting the stimuli used in a particular experiment are approximately 'orthogonalized' (as shown by the solid lines) by the scaling factor. The scaling factor is interpreted as reflecting an adaptive weighting depending on the particular stimulus set used*

in the two experiments. Background colour is indicated by a grey cross. R: Red, G: Green, B: Blue, Y: Yellow, L: Lime, P: Purple.

The observed attentional effects are re-plotted in Figure 7 in solid black while the predicted effects are plotted in colour, with error bars indicating the 95% confidence intervals. Goodness of fit ('error'; shown in table 2) was slightly better for experiment 1 (red, blue, green, yellow) with all means falling within or very close to the confidence intervals, and somewhat worse for experiment 2 (red, purple, blue, lime), in which one data point was clearly not predicted by the model. Model fits were extremely poor when the scale factor was fitted simultaneously for both experiments. We interpret this as evidence that the scaling of the chromatic mechanisms underlying the colour distances may depend on the colour stimuli used in a particular experiment, consistent with experiments demonstrating flexible chromatic weights resulting from exposure to different chromatic environments (Neitz et al., 2002).

The aim of our modelling was to further understand some of the variability between colours. While attentional effects were lowest for non-separable targets and remained close to 0 (Figure 5), our model fits demonstrate that target proximity suffices to explain the attentional effects if one allows an adaptive scaling of the chromatic axes contingent on the colours used in the experiment.

4. General Discussion

This study examined behavioural and neural markers of divided attention within the feature dimension of colour, requiring participants to attend concurrently to two out of four continuously present colours, with allocations of attention assessed by recordings of SSVEPs.

We found reliable attentional increases in SSVEP amplitudes in two separate experiments (see Fig.6), demonstrating that simultaneous selection of two feature values from the same dimension can be implemented at an early neural level even when attended and unattended values are not spatially separated. We also observed significant differences in the efficiency of selection that depended on both the context of target/distractor chromaticities and the linear separability of colours in hue space. However, while linear separability is not sufficient to explain the attentional effects, target proximity can account for the attentional effects if one allows an adaptive scaling of the chromatic axes contingent on the colours used in the experiment. These data are consistent with previous reports that colour selection in multi-coloured displays operates on the output of higher-order chromatic mechanisms (Nagy and Thomas, 2003). Our modelling of SSVEP attentional effects using distances in colour space allowed for a more fine-grained account of the magnitudes of attention effects and suggests a context-dependent, flexible scaling of chromatic axes for the purpose of attentional selection.

Attentional effects depended strongly upon the particular combination of attended colours, even though all colours were clearly distinguishable. Thus, these data do not support the idea that colour categories might constitute separate attentional feature dimensions that can be selected independently. If, for example, attentional weights could be set independently for each of the four unique hues, attentional enhancement should have been consistently observed for all the hue combinations. The overall magnitude of attentional effects did not differ much between the first experiment and the second experiment, further suggesting that unique hues are not special for enabling attentional selection (see supplementary material for

convergent behavioural evidence). Our data also seem inconsistent with attentional weights affecting the gain of colour opponent mechanisms, as this would have allowed for better than observed selection of non-separable colour pairs in the experiment with unique hues. Instead, the variability of attention effects in our data was well-described by a simple model that depended upon the configuration of target / distractor colours and their distances in colour space. This suggests that for attentional purposes, colour should be regarded as a single feature dimension, without further subdivisions based on hue categories. This is conceptually analogous to spatial attention, which has been likened to a spotlight in 2D space (Posner, 1980) rather than the superimposition of two independent attentional mechanisms for selection of vertical and horizontal position. The spotlight or zoom lens analogy could also explain the lack of an attentional effect for linearly non-separable distractors, since the intermediate distractor would also be amplified, as well as the finding of greater attentional effects for closer target-target proximities, which could be related to a more focused zoom lens. Such predictions could be derived from the neural-level model proposed by Pestilli and colleagues (2011).

The SSVEP attentional enhancement showed a clear reduction for conditions that involved targets that were not linearly separable from distractors in colour space. These reductions were present in both experiments, indicating their generality across colour contexts. SSVEP attentional effects were generally reduced for the non-separable colour combinations, with Figure 5 showing the effects to include zero well within their 95% confidence intervals for most of such colour combinations. In our model, reduced attentional enhancements for certain colour pairs lead to different relative scaling of the contributions of

the two opponent chromatic mechanisms between the two experiments, with orthogonalisation of non-separable colours as the most obvious outcome (Fig. 9). The lack of SSVEP enhancement for simultaneous selection of non-separable hues (e.g., red and green targets in the presence of yellow and blue distractors) may be due to the failure to achieve cortical enhancement of their discrete colour representations. Around 50% of cells in the early visual areas of macaque monkeys are estimated to be colour-selective, with little difference between V1, V2, V3 and V4. The majority of neurons in V1-V3 are broadly tuned to colour (for a review, see Gegenfurtner, 2003; see also Xiao et al., 2007; Xiao et al., 2003); V1-V3 are the sites that are likely to give rise to the SSVEP effects we observe in our study (for source localisation of SSVEP attentional effects using the same task, see Müller et al., 2006). Therefore, it is not surprising that chromatic proximity, in particular in terms of colour differences in a uniform hue space, is relevant for attentional selection at an early neural level. This is also in line with some recent models of attentional selection effects on early neural populations (e.g. Verghese et al., 2012).

Clear interpretation of the observed behavioural effects as an outcome of attentional enhancement is somewhat complicated by the fact that performance in the coherent-motion target detection task was also considerably influenced by the flicker frequency. Furthermore, in the behavioural data, it is not possible to fully disentangle the relative contribution of each colour to observed data patterns, while SSVEPs allow monitoring of attentional processing for each individual colour throughout the experiment. Nonetheless, some salient differences did emerge between colour target pairs even in the behavioural data. In experiment 1 (red, blue, green, yellow), higher false alarm rates were observed when attending red/green (a

colour pair that was not linearly separable from blue/yellow distractors), and this was associated with a more liberal criterion of responding. From Figure 2a, it can be observed that yellow is relatively close to red/green in MB space, so the inability to filter out yellow distractors was likely to be the cause of this effect (for consistent effects of higher false alarms for non-separable colours in the absence of flicker, see Supplementary Material 1). In experiment 2 (red, purple, blue, lime), higher hit rates and a tendency towards a more liberal response criterion were observed for attending purple/blue as opposed to lime/red. While purple/blue and lime/red are roughly similar in their distances in MB colour space, they differ in perceptual hue space, with lime being the most distant distractor. Thus, based on our behavioural data, effects were found that are consistent with both cone-opponent and hue-based influences. Furthermore, hit and false alarm rates observed here are roughly comparable to those observed when participants were cued to attend to two out of four overlapping stimuli based on either colour or orientation in a previous study using the same task (hit rate: 63%, false alarm rate: 17% Andersen et al., 2015). Despite differences between these studies, the overall comparable task-performance suggests that attentional selection of two colours might not be all that more difficult in behavioural terms than selection of a single colour. This conclusion is consistent with the findings of Andersen et al. (2013), who observed modest costs for attending to two different colours in the left and right visual fields as long as the same colour didn't have to be attended at one location and ignored at the other location. The present study extends this finding by demonstrating concurrent attentional selection of two colours at the same location.

Although we did not observe any behavioural costs associated with colours that contain large S-cone signals (blue and purple), as would be predicted by the findings of Lindsey et al. (2010), attentional enhancement of SSVEPs was greatly reduced or even absent for blue and purple. This could be taken as evidence for an early locus of the S-cone increment disadvantage observed in that study. Wool et al. (2015) reported an increased salience of S-cone decrements (yellowish) as opposed to S-cone increments (bluish) and discussed the possibility that greater response compression of the S-cone increments may correlate with lower perceived saturation. Lack of attentional enhancement for S-cone increments in early visual areas has also been reported by Wang and Wade (2011). It has been speculated that the cortical amplification of $S/(L+M)$ signals occurs in V1 through recurrent circuits or lateral excitatory circuits of neurons with proximal receptive fields (DeValois et al., 2000). As discussed by Martinovic and Andersen (2018), who report that S-cone and luminance signals are processed more independently in the cortex, the need to amplify S-cone signals relatively early in order to compensate for their reduced sub-cortical representation (Mullen et al., 2008) may introduce a cost to the subsequent amplification of these signals through recurrent circuitry. Previous SSVEP studies (reviewed in Andersen et al., 2011b) reported robust attentional effects for blue, but they relied on relatively low luminance colours driven by single monitor phosphors and thus not only more removed from the S-(L+M) axis but also much more saturated than the current stimuli or stimuli from Martinovic and Andersen (2018). The dependence of attentional enhancements for S-cone (bluish) colours on saturation at various lightness levels lies beyond the scope of the present study, but it certainly warrants further investigation.

Together with lower attentional modulation of SSVEP amplitudes for blue and purple, we also observed considerable variation in the magnitude of attentional effects for other colours. For example, in experiment 1 (red, blue, green, yellow), red attended with yellow received a high boost in amplitude, but a lower boost was observed when red was attended with blue, even though the attended colours were linearly separable from their distractors in both cases (see Figure 5). We attempted to account for these differences by a model based on target proximity and distractor distance in colour space. Our model fits suggest that colour distances are used in a different way depending on the target/distractor chromatic context, consistent with previous experiments demonstrating flexible chromatic weights resulting from exposure to different chromatic environments (Neitz et al., 2002). From the perspective of the normalisation model of attention (Reynolds & Heeger, 2009), our data suggest that the ‘attention field’ can be divided in colour space. This would maximise the differences in neural responses elicited by target as opposed to distractor colours (Pestilli et al., 2011). The difficulty in selecting non-separable colours might result from the relatively broad tuning of many colour sensitive neurons in V1-V3 (Gegenfurtner, 2003; Xiao et al., 2007; Xiao et al., 2003) and the rather modest attentional sharpening of tuning curves (Reynolds & Heeger, 2009). To account for these effects our model incorporates an adaptive scaling of the chromatic axes contingent on the colours used in the experiment, resulting in orthogonalization of non-separable colours. Our model thus explains attentional selection of colour as maximisation of colour space distances between neighbouring colours given the provided colour context and is thus able to explain all the observed attentional effects through target proximity alone.

To our knowledge, the present study is the first to demonstrate convincingly that dividing attention across multiple co-localised feature values belonging to a single feature dimension can lead to the enhancement of neural markers of attentional selection for the attended feature values. The extent of enhancement was larger both when attended colours were more similar and when they were linearly separable in colour space from their distractor colours. Although linear separability is conceptually not fully reducible to target proximity, target proximity suffices to explain the attentional effects if one allows an adaptive scaling of the chromatic axes contingent on the colour context. This result is inconsistent with the idea that attention can be allocated independently to different hues at the same time and suggests that colour should be considered a single feature dimension for attentional purposes, at least when it comes to hue.

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Author contributions

JM, SKA, SMW, MMM and SAH designed the experiments and wrote the manuscript; JM and SKA implemented the paradigm; JM collected and analysed the data; JM and SMW designed the model; SMW performed the modelling.

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