Attention to Colour: Spotlight in Hue Space

Abbreviated title: Hue space spotlight

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No of pages: 27
No of figures: 5
No of tables: 1

Word counts - Abstract: 239, Introduction: 649, Discussion: 1422

Acknowledgments. AB was supported by a BBSRC Eastbio research experience placement to work in the lab of JM through the Doctoral Training Programme BB/M010996/1. The authors state no conflict of interest. For the purpose of open access, the authors have applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising from this submission.

Author contributions: JM designed the experiment; JM and SKA implemented the experimental and analysis scripts; AB and JM collected the data; JM analysed the data; AB, JM and SKA wrote the manuscript.

Abstract

Biological systems must allocate limited perceptual resources to relevant elements in their environment. In vision, this can be achieved by attending to a spatial location or a defining feature (e.g. colour). Spatial attention can be conceived as a spotlight in 2D space, whose focus can differ in breadth and concentration. Could attention to colour also function as a spotlight that highlights an area of colour space? We examined this in an experiment that used multicoloured displays with four overlapping random dot kinematograms (RDKs) that differed only in hue. We manipulated (1) requirement to focus attention to a single colour (red or green) or divide it between two colours (red and green); (2) distances of distractor hues from target hues. This resulted in three different colour contexts, which differed in proximity between targets and distractors. We conducted a behavioural and an electroencephalographic experiment, in which each colour was tagged by a specific flicker frequency and driving its own steady-state visual evoked potential. Behavioural and neural indices of attention showed several major consistencies. Concurrent selection of red and green reduced the efficiency of target enhancement and produced context-dependent distractor interference, consistent with a combination of two hue-selective spotlights of unchanged breadth but reduced concentration. This conceptual similarity in implementation of spatial and feature-based selection implies that attentional modulation of signals in biological systems is likely to be implemented using the same domain-general selective mechanisms, which are well-described with a spotlight metaphor.

Significance statement

Attention selection of spatial locations and visual features (e.g. colour) is implemented through different neural mechanisms – spatial attention selects all features in the attended location, while feature-based attention selects attended features across the visual field. However, these selection mechanisms also share similarities. Our study on colour-based attention demonstrates that the spotlight metaphor applied in hue-space can adequately explain obtained patterns of behavioural and neurophysiological data. This hints at universal, domain-general mechanisms of selection, determining its efficiency relative to the number of to-be-selected targets and their proximity to other elements in the scene, be it by spatial location or distance (i.e. similarity) in featural space.

Introduction

Biological systems need to allocate limited perceptual resources to relevant elements in their environment. In vision, this is achieved through spatial (Eriksen & St. James, 1986; Posner, Snyder, & Davidson, 1980), feature-based (Treue & Martinez-Trujillo, 1999) or object-based attention (Duncan, 1984). It is widely accepted that spatial attention can operate as a spotlight in 2D space (Brefczynski & DeYoe, 1999). In fact, the spotlight metaphor was extremely valuable in guiding the development of quantitative models of attention (Cave & Bichot, 1999). Yet, despite decades of research, we still lack a comprehensive model or a useful hypothesis-generating metaphor on how feature-based attention may operate within the continuous domain of a complex, multi-dimensional feature space such as colour (although see Stormer & Alvarez, 2014).

Here, we ask the following question: could attention to colour be distributed in the form of a spotlight that highlights an area of continuous colour space, similarly to a spatial spotlight? This is an interesting proposition, emerging from recent neuroscientific work on concurrent selection of multiple hues (Martinovic, Wuerger, Hillyard, Müller, & Andersen, 2018). Martinovic and colleagues (2018) demonstrated that 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. The magnitude of attentional 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 support attentional selection. Such adaptive rescaling is consistent with a series of recent studies that show attention optimally biases neural responses depending on several factors: the tuning of sensory neurons, physical

characteristics of the visual environment and the nature of the task (Scolari, Byers, & Serences, 2012; Scolari & Serences, 2009; Verghese, Kim, & Wade, 2012).

To fully assess how feature-based attentional selection works for individual colours in a display with multiple targets and distractors, it is optimal to be able to record an individual response for each colour. We achieved this, by using a multi-colour random dot kinematogram (RDK) display in combination with frequency-tagging, allowing us to look at the neural markers of attentional processing for 4 colours simultaneously. This is a well-established procedure for studying the neural markers of feature-based attention (e.g., Andersen, Fuchs, & Muller, 2011; Andersen, Hillyard, & Muller, 2013; Andersen & Muller, 2010; Andersen, Muller, & Hillyard, 2015; Andersen, Muller, & Martinovic, 2012). The colours differed in hue but were of constant lightness and colourfulness, as specified in a perceptually uniform colour space (CIE Lab; see Fairchild, 2013).

We measured neural activity elicited by each colour in a 4-colour display when attention was focused on red or green or divided between red and green in order to detect infrequent coherent motion events in these colours. To generate different stimulus contexts in which these targets would need to be selected, we manipulated distances between targets and one of the distractor hues. This resulted in three contexts: i) a neutral context, with intermediate distractors falling between the two target hues (blue and yellow); ii) a context with one distractor closer to red (orange and yellow); iii) a context with one distractor closer to green (lime and yellow). We measured neural and behavioural outcomes of attention to single or multiple colours using the same paradigm with and without flicker. If colour selection relies on the same type of spotlight as spatial selection, we should observe costs of attending to multiple colours in terms of increased distraction – behaviourally, by reduced sensitivity to signal colour; neurophysiologically, by SSVEP amplitudes driven by targets

being reduced and/or SSVEP amplitudes driven by distractors being increased - when going from single-target selection to two-target selection. This would imply that attentional modulation of signals in biological systems is implemented using the same type of domain-general mechanisms, which are well captured by the spotlight metaphor.

Materials and Methods

Participants

Twenty-five volunteers in total took part in the study, but five were removed from the final sample. One participant was excluded due to technical problems during the EEG recording. Four other participants were excluded due to poor task performance in the EEG session (identified as d's < 0 in any of the conditions). The remaining 20 participants (4 male) were on average 23 years old (range 21–27 years). With a sample size of 20 participants and a significance level of 0.05, a paired samples t-test would yield 80% power with an effect size of d=0.66 (calculated with package pwr for R; Champely et al., 2020). In light of previous work in the field, which generally reports large effects of attention on SSVEP amplitudes (>0.8; e.g. Andersen, Hillyard, & Muller, 2008; Andersen et al., 2012) this was deemed to be a sufficiently large sample.

All participants were right-handed and had normal or corrected-to-normal vision and normal colour vision as assessed by the Cambridge Colour vision test (CCT; Regan, Reffin, & Mollon, 1994). All participants reported having no neurological or psychiatric history and gave written informed consent prior to testing. Participants were recruited amongst the University of Aberdeen students and were reimbursed for their time and effort. The study was approved by the ethics committee of the School of Psychology, University of Aberdeen and was in line with the Declaration of Helsinki (2013).

Stimuli and Procedure

Stimuli were presented on a 21-inch ViewSonic P227f CRT monitor, calibrated using a ColorCAL 2 (CRS, UK) and controlled by a VISaGe (CRS, UK) system. The resolution was set to 640 x 480 pixels with a refresh rate of 120 Hz. CRS toolbox and CRS colour toolbox for Matlab (Mathworks, USA) were used to run the experiment. Colour conversions were based on 1931 colour matching functions and measurements of the spectra of the monitor phosphors taken by a SpectroCAL (CRS, UK). The viewing distance was approximately 70 cm. The behavioural session was done in a dark room and the EEG session in an electrically shielded, sound-attenuated chamber. The monitor was the only source of light.

Table 1. Stimulus and background colour coordinates in CIELCh and CIE 1931.

Colour	CIELCh			CIE 1931		
	L	C	h	x	y	Y
Red	60	34	0	0.380	0.297	28.12
Green	60	34	180	0.247	0.361	28.12
Yellow	60	34	90	0.397	0.418	28.12
Blue	60	34	270	0.230	0.242	28.12
Orange	60	34	45	0.425	0.361	28.12
Lime	60	34	135	0.322	0.426	28.12
Background	55	0	0	0.313	0.329	23.00

The stimuli used were four fully overlapping random dot kinematograms (RDKs) that differed in hue (0°, 180°, 90°, 270°, 45° and 135°, corresponding to red, green, yellow, blue,

orange and lime; see Table 1) but were of equal chroma and lightness in CIE LCh space (C=34 and L=60). Perceptual colour spaces are continuous 3D spaces with the dimensions of hue, colourfulness and lightness (e.g., CIELAB, CIELUV; Fairchild, 2013). Euclidean distance (ΔE) between two points in these spaces is taken to be a measure of their perceptual colour difference, with a just-noticeable difference being equal to a ΔE of 2.3. CIELAB space is sometimes used in studies on colour-based attention under the assumption that it is fully perceptually uniform and therefore enables researchers to collapse data across individual colours, as long as same colour distances between targets and distractors are used (e.g. Stormer & Alvarez, 2014). However, while CIELAB does a decent job at representing appearance of colours, it is worth noting that the perceptual unique hues (red, green, yellow and blue) do not align directly with the CIELAB axes (Fairchild, 2013). This is why in our previous study, which aimed to establish whether it is possible to divide feature-based attention along the dimension of colour, we defined our stimuli on the basis of normative unique hue data rather than CIELAB space (Martinovic et al., 2018). Assuming illumination equivalent to D65, unique hues lie approximately at CIELAB hue angles of 24° (red), 90° (yellow), 162° (green), and 246° (blue) (Fairchild, 1996; for an in-depth analysis, see Seymour, 2020; Figure 1a). Despite these caveats, CIELAB is well suited for the current study because it provides a space in which relative perceptual distances between hues can be easily controlled, while ensuring that saturation, colourfulness and lightness remain constant across samples (Schiller, Valsecchi, & Gegenfurtner, 2018).

The approximate appearance of the stimuli is depicted in Figure 1, together with the trial outlook. Colours were presented in three possible colour contexts. In the first context, the colours were equally spread in CIELAB space (red, yellow, green and blue). In the second context, we kept the yellow distractor and replaced the blue distractor with orange, to place it closer to red (red, orange, yellow and green). Lastly, in the third context, the blue

distractor was replaced with lime, to place it closer to green (red, yellow, lime and green). Rather than deploying distractors and targets pooled from different sections of the CIELAB as in Stormer and Alvarez (2014), we opted to evaluate in detail shifts within one quadrant of the colour space. This allows us to quantify any hue-specific non-uniformities. Within our design, the yellow distractor served as an important comparison point both between and within colour contexts. Meanwhile, the orange and lime distractors are both placed in the same half of hue space but occupy a position nearer to one of the targets (red and green, respectively). The background was metameric to D65 (CIE 1931 coordinates: x=0.3128, y=0.3290, Y=23 cd/m^2).

For the EEG session each colour was tagged with a specific flicker frequency. The colour red flickered at 8.57 Hz; green at 10 Hz; yellow at 12 Hz and depending on the context either blue, orange or lime at 15 Hz. These frequencies correspond to flicker cycles of 14, 12, 10, and 8 frames, respectively, at our 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 same flicker frequencies yielded valid findings in a series of previous studies (for a summary, see Martinovic et al., 2018). Advantages and disadvantages of counterbalancing colour-to-frequency allocations are also discussed more extensively in that paper and will only be briefly summarised here: the benefits of counterbalancing would be outweighed by more practical costs, with loss of precision of SSVEP measurement that would result from the two-step process of averaging trials stemming from different frequencies (first, average within the same frequency; second, normalise and collapse across frequencies).

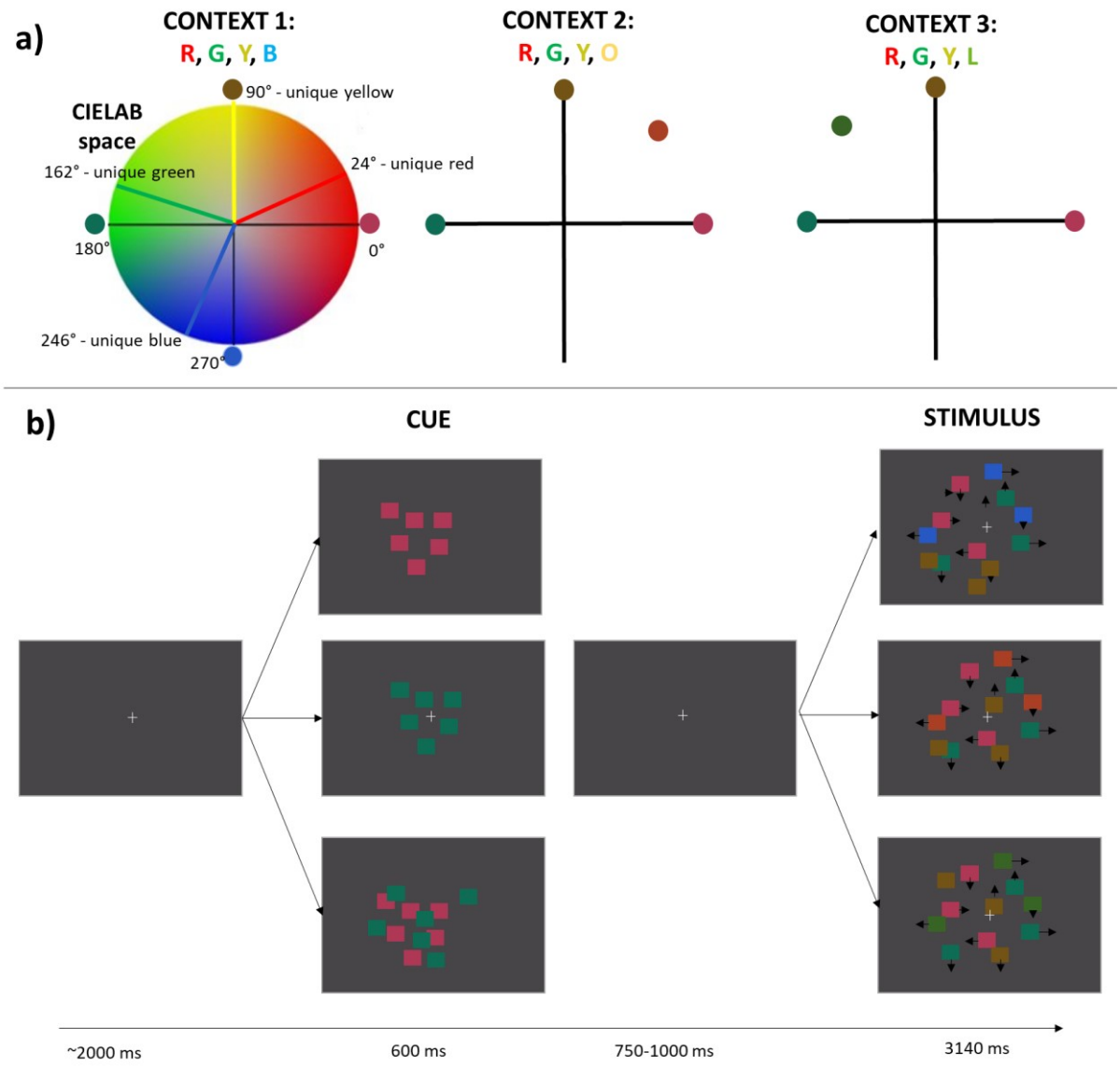

Figure 1. Stimulus colours and trial outlook. *A) Stimulus colours. Colours were selected from the perceptually uniform CIELAB space (see Table 1 for coordinates) to generate three sets of contexts. Red and Green were targets in each context. Yellow was the fixed distractor, also present in each context. There were three context-specific distractor colours: 1) blue, generating a context with equally spaced colours in CIELAB; 2) orange, generating a context in which a distractor was closer to the red target; and 3) lime, generating a context in which a distractor was closer to the green target. The positions of unique hues under illuminant*

D65 as described by Fairchild (2013; e.g. a yellow that is neither red nor green) are indicated in relation to CIELAB axes. B) Trial outlook. Participants were cued to attend either red or green alone or both colours simultaneously. After a delay of 0.75–1.0 s they observed a stimulus interval with the four colour RDKs intermingled spatially and moving at random. Each stimulus interval could contain between 0 and 3 brief coherent movements (left, right, up or down) of either the attended or the unattended colours. In the figure, the number of dots is reduced for the sake of clarity. Colours cannot appear exactly as they did on a calibrated display but have been adjusted to closely resemble their appearance in sRGB space (i.e. for on-screen viewing).

The field occupied by the random dot stimuli extended over a circular area with a diameter of 15.642°. Each of the four colours was represented by 75 squares of 0.391° of visual angle, which made 0.061° displacements per frame in a random direction. The squares were drawn in random order to prevent systematic overlap. At the start of each trial a white fixation cross (0.488° by 0.488°) was presented for about 2 seconds, followed by the presentation of a cue that lasted 600 ms. The cue instructed participants to attend to one colour (either red or green) or two colours (both red and green), by presenting a static frame of dots in the to-be-attended colour(s). The cue was followed by 0.75-1 seconds of fixation prior to the motion interval with all four RDKs, which lasted 3.14 seconds. The motion display also contained the fixation cross and participants were instructed to maintain their gaze at fixation throughout each trial. Target and distractor coherent motion events were embedded within Brownian-like dot motion. Participants used a CT-6 button box (CRS, UK) and were instructed to respond to coherent motion of the cued colour(s), whilst ignoring any such motion from uncued colours. A coherent motion lasted 400 ms and consisted of 50% of the dots from the same colour, randomly selected on 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. Responses that occurred within 250-900 ms after the onset of coherent motion events in attended or unattended dots 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.

The experiment consisted of two separate sessions: a behavioural and an EEG session. The main differences between them were (1) the inclusion of flicker-frequency tagging and (2) the reduction in the number of coherent motion events in the EEG session, aimed at capturing attention-related processing using SSVEPs (for a review, see Andersen, Müller, & Hillyard, 2011). Before the start of the behavioural session, participants were asked to do a practice block of 40 trials. During practice they were provided with feedback sounds: a low beep (600 Hz) corresponded to an incorrect response (false alarm/miss) and a high beep (1500 Hz) indicated a correct response (hit). Prior to the EEG recording, participants did another practice set of 15 trials to familiarise themselves with the now flickering stimuli. For the behavioural session, participants performed 270 trials, with 30 trials for each of the nine conditions (3 attentional conditions x 3 colour contexts). All of the trials contained between 1 and 3 coherent motion events, resulting in 540 events in total and 60 events per condition (15 per colour). In the EEG session there were a total of 405 trials (45 per condition), of which 30 contained no events and 15 had between 1 and 3 events.

The completion of the behavioural session, including the colour vision test and one practice block took approximately an hour. The EEG session lasted about 2½ hours, with the recording lasting approximately 1 hour and the rest of the time devoted to the brief practice block and electrode setup and removal.

Experimental Design and Statistical Analysis

Behavioural data

To establish how attentional focus and stimulus context affected participant performance, we analysed hit rates, false alarm (FA) rates and response biases. We used criterion (c) as the most basic measure of response bias, combining false alarms across distractor colours into a single FA rate and the hits across the two targets into a single hit rate (for divided attention) prior to the calculation. When false alarm and hit rates sum to 100% c = 0, if both are 0.99 then c = -2.33 and if both equal 0.01 then c = 2.33 (Macmillan & Creelman, 2004). Thus, criterion below 0 reflects a liberal response pattern (FAs exceed misses) and criterion above 0 reflects a conservative response pattern (misses exceed FAs). Prior to calculating the criterion, hit rates of 100% and FA rates of 0% were adjusted according to Wickens' (2002) proposal, which assumes that should the number of trials have been doubled, at least one hit or FA would have been observed.

On hit rates, we conducted a 3x2x2 repeated measures ANOVA with factors *context (yellow/blue, yellow/orange or yellow/lime), attentional focus (focused on a single target or split between two targets)* and *target colour from which responses are analysed (red or green).* For the false alarm rates, a 3x3x2 repeated measures ANOVA was performed, with factors *context (yellow/blue, yellow/orange or yellow/lime), attentional focus (to red, green or both targets)* and *distractor colour from which responses are analysed (fixed: yellow, changing: blue, orange or lime).* While plots depict uncorrected hit and FA rates, statistical analyses were performed on their inverse normal transform after correction according to Wickens (2002), to ensure that their limited range (0-100%) does not cause spurious interactions.

When red and green were attended on their own, these two colours would also act as distractors. False alarm rates driven by these red and green distractors were investigated by performing a 3x2 repeated measures ANOVA, with factors *context (yellow/blue,*

yellow/orange or yellow/lime) and distractor colour (red or green). This control analysis aimed to verify if the target colours were equally effective when they adopted the role of a distractor. Having selected two colours from the opposite sides of the colour space, we expected that this would be the case.

Finally, we performed a 3x3 repeated measures ANOVA on the criterion, with factors of *context* (yellow/blue, yellow/orange and yellow/lime) and *attentional focus* (red, green and split between the two). The criterion is informative on whether attention to multiple targets leads to a change in the position of the 'decision axis' about the presence or absence of the signal. The number of target events when attention is divided across two colours increased from 25% to 50% of all coherent motion events, while the number of distractor events fell from 75% to 50%. Target prevalence influences response criterion rather than sensitivity (i.e. d') as it leads to trade-offs between misses and FAs (Wolfe & Van Wert, 2010). In figure 2a depicting the results from Wolfe & Van Wert's (2010) visual search study, the shift in criterion remains negligible when manipulating target prevalence between 25% and 50%. Nevertheless, quantifying the criterion in addition to the hit and FA rates will allow for a more balanced interpretation of the behavioural findings.

Statistical analyses were performed in IBM SPSS Statistics for Windows version 27. If three-way interactions were found in the ANOVAs, they were followed up with multiple two-way ANOVAs. Greenhouse-Geisser correction of the degrees of freedom was used when the assumption of sphericity was violated. Post-hoc analyses of two-way interactions and main effects themselves were performed using Bonferroni-Holm corrected paired t-tests. The same analyses of hit rates, false alarm rates and criteria were applied to the behavioural data extracted from the EEG session.

EEG recording, processing and analysis.

Brain electrical activity was recorded at a sampling rate of 256 Hz from 64 Ag/AgCl electrodes using a Biosemi ActiveTwo EEG system (BioSemi, Netherlands). Lateral eye movements were monitored with a bipolar outer canthus montage (horizontal electrooculogram). Vertical eye movements and blinks were monitored with a bipolar montage positioned below and above the left eye (vertical electrooculogram). During recordings, the CMS (Common Mode Sense) and DRL (Driven Right Leg) electrodes were used to drive the average potential for each participant as close as possible to the AD-box reference.

EEG data were processed using the EEGLab toolbox (Delorme & Makeig, 2004) in combination with custom-made procedures in Matlab (The Mathworks, Natick, MA). 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 analysed data were not contaminated by activity related to coherent motion or manual responses and left a total of 30 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%, leaving an average of 27 trials per condition for analysis (range 14-30). 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. Attentional effects were computed by subtracting amplitude when unattended from amplitude when attended (A-U). To investigate how the attentional increase in SSVEP amplitudes was influenced by the different conditions of the experiment, we performed a 3x2x2 repeated measures ANOVA on the strength of the attentional effect (A-U) with factors *attentional focus (to a single target or divided between two targets), context (yellow/blue, yellow/orange or yellow/lime)* and *target colour from which responses are analysed (red or green)*. Since the changeable distractors were physically different (blue, orange and lime) and thus elicited vastly different amplitudes (consistent with e.g. Martinovic & Andersen, 2018; Martinovic et al., 2018), the distractor-driven amplitudes could not be fully compared between contexts. To investigate how distractors were processed between contexts, we therefore focused exclusively on the SSVEP amplitude elicited by yellow, which was the distractor that was constantly present. A 3x3 repeated measures ANOVA with factors of *context (yellow/blue, yellow/orange or yellow/lime),* and *attentional focus (to red, green or split)* was conducted. We also conducted a repeated measures ANOVA with factor *attentional focus (red, green or split)* on amplitudes driven by each of the context-specific distractor colours (blue, orange and lime) to reveal whether their neural processing was affected by the target colour(s).

Finally, to understand the properties of the putative hue-selective spotlights more fully, we further evaluated differences in amplitudes between single-target and dual-target selection. Our simple, mechanistic application of the spotlight metaphor to hue-space is depicted in Figure 2, positing a selection beam that is applied to an area of the colour space and modulates the processing of neurons that respond to the hue(s) within the beam.

Attentional settings for colour are influenced by their categorical status (Found & Muller, 1996) which can be used to set selection weights relative to the other colours in the display (e.g. 'redder than' or 'yellower than'; Becker, 2010). In Figure 2, this breadth of target-representation tuning is represented by a relatively wide spotlight, encompassing an area of +/- 45° in colour space (for similar colour tuning in visual working memory, see Bays, Catalao, & Husain, 2009). A simple mechanistic model, in which a transition from one to two spotlights would reduce the processing resources in half, would predict that the attentional effect should be halved when combining the two attentional settings. This is equivalent to evaluating a mean-amplitude model in which amplitude when selecting two features concurrently is equal to the average of amplitudes when attending single feature values individually (for similar findings from orientation and colour, see Andersen et al., 2015; Andersen, Müller, & Hillyard, 2009). The mathematical equivalence of these statistical tests stems from the fact that attentional increases when attending red alone or together with green are calculated by subtracting the same unattended amplitude (i.e. red when green is attended). Thus, despite the values being different, the statistical comparison relies on the identical underlying data (i.e. testing if $(AmpR_{,r} + AmpR_g) / 2 = AmpDiv_r$ vs. $(AmpR_r – AmpR_g) / 2 = AmpDiv_r – AmpR_g$ where $AmpR_r$ is amplitude for red when attending red, $AmpR_g$ is amplitude for red when attending green and $AmpDiv_r$ is amplitude for red when dividing attention). Similarly, we predicted amplitudes for each context and each distractor colour in dual-target conditions by averaging the amplitudes driven by those colours in single-target conditions. These predictions were evaluated by paired t-test comparisons between predicted and observed data when attention was divided.

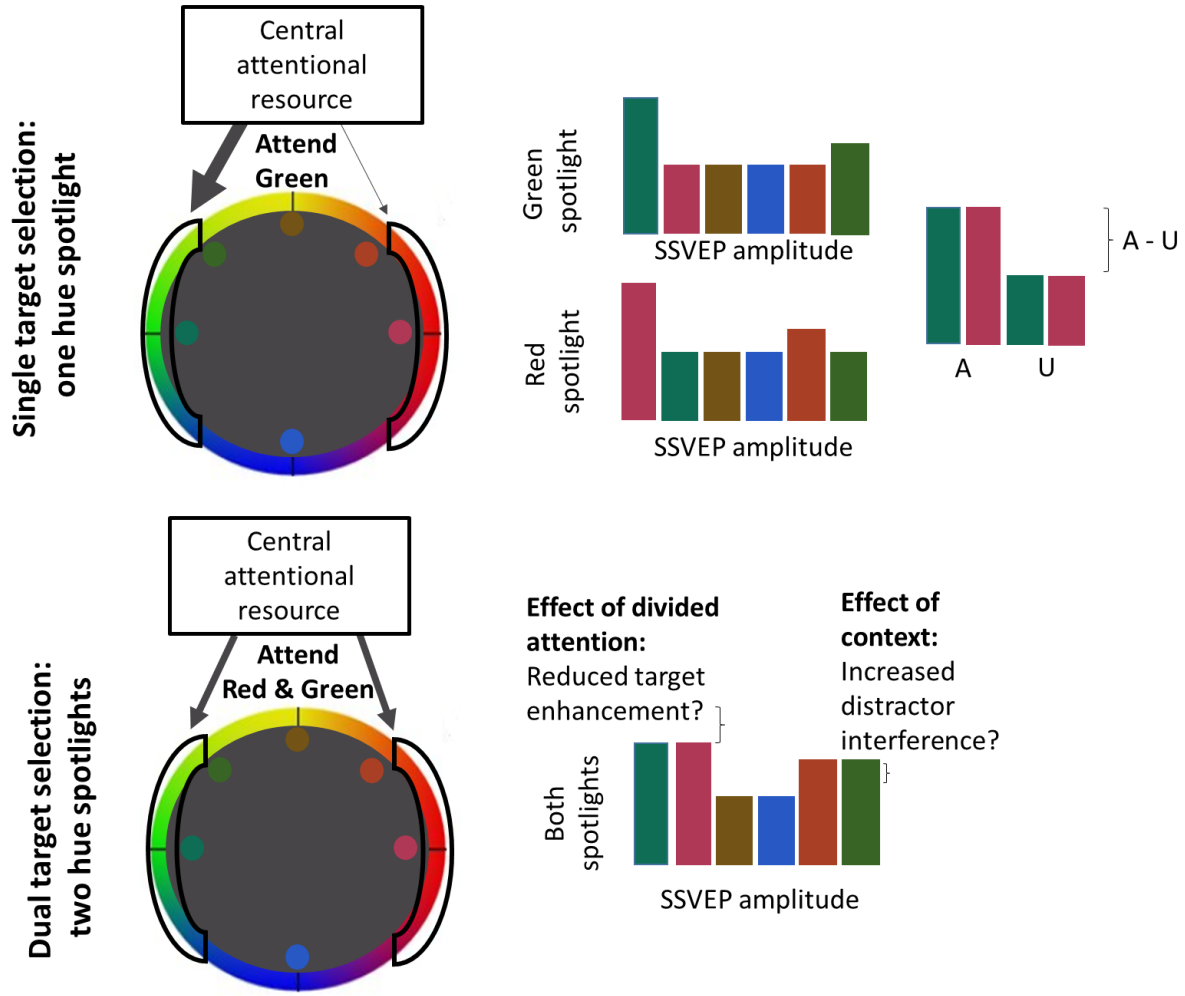

Figure 2. Spotlight in hue space: A simple model for attentional processing of hue*. A spotlight applied in hue-space would affect processing within all neural units that respond to the target representation. As depicted on the top panel, a single spotlight would enhance neural processing of colours within the region of hue-space highlighted by the spotlight – in our case, the red or green target and their proximal distractors (e.g., orange when red is attended). The attentional effect is computed by subtracting amplitude for a target (e.g. red) when it is ignored from its amplitude when it is attended. As depicted on the lower panel, application of two spotlights should lead to reduced target processing and might also lead to increased distractor processing.*

Results

Behavioural experiment

Collapsing the data across all stimuli and conditions yields hit rates of 78% ± 12%, false alarm rates of 6% ± 5%, with a criterion of 0.36 ± 0.27 (means and standard deviations). This shows that the motion detection task is challenging but achievable, reflected by the high percentage of hits and the low rate of false alarms. A positive but relatively small bias indicates that participants adopted a somewhat conservative strategy. Hit rates, false alarm rates and criteria are depicted in Figure 3a.

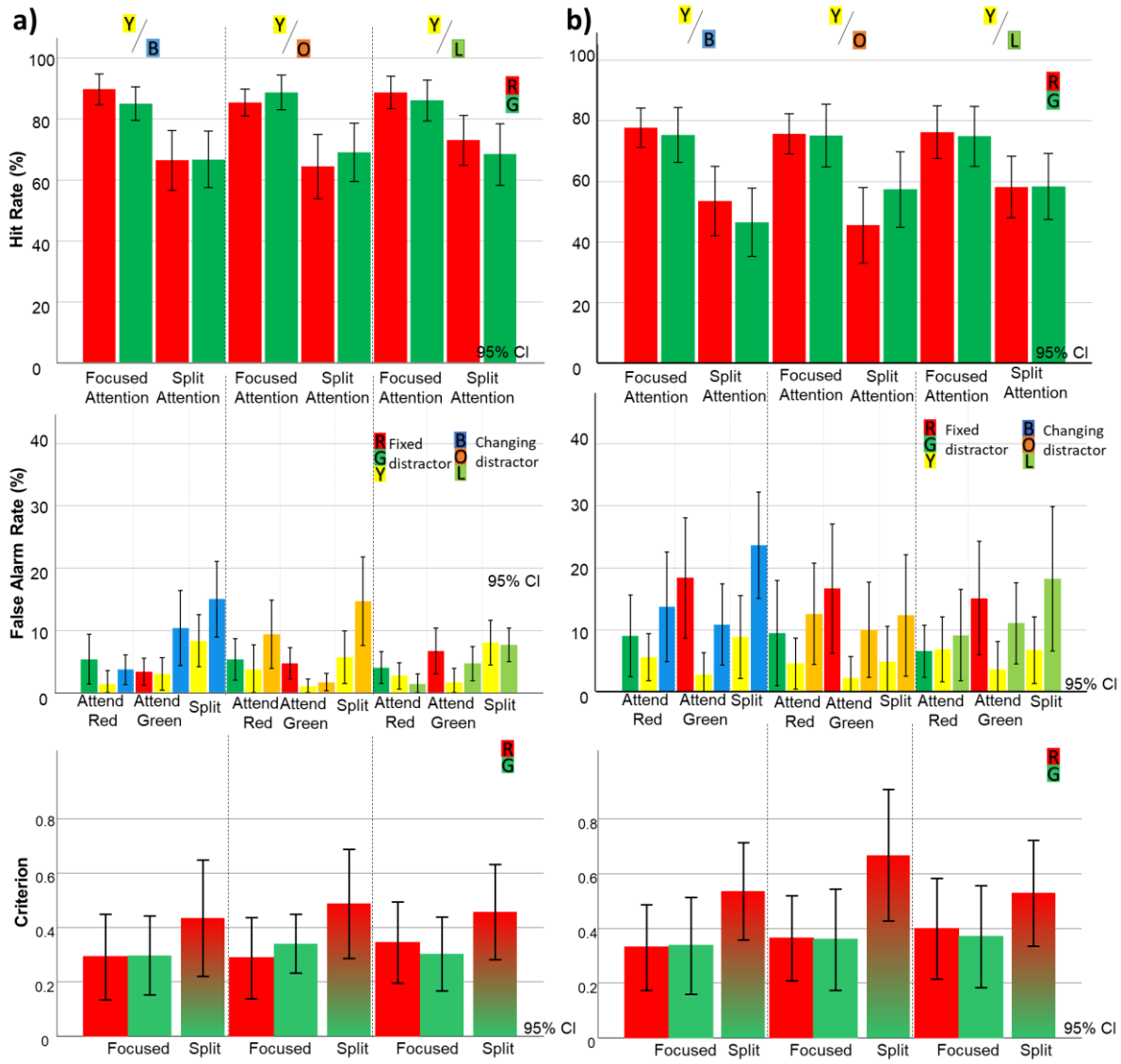

Figure 3. Behavioural results: Hit rates (top panel), False Alarm rates (middle panel) and criteria (bottom panel). A. *Behavioural Experiment (without flicker).* ***B.*** *EEG Experiment (with flicker). Conditions are organised based on the three contexts, with the following distractors: yellow/blue, yellow/orange and yellow/lime. Within the panels A and B, the contexts are always grouped in this order. Attention could be focused on a single target colour (i.e. red or green) or divided across these two targets (i.e. split). Error bars depict 95% between-subject CIs.*

Hit rates (Fig.3a, top panel) were subjected to a 3x2x2 repeated measures ANOVA with the following factors - *context (yellow/blue, yellow/orange or yellow/lime), attentional focus (focused on a single target or split between two targets)* and *target colour (red or green)*. When participants were asked to focus attention on a single target-colour, the hit rate was higher as opposed to when they were asked to divide attention across the two colours (main effect *attentional focus* ($F(1, 19) = 28.54$, $p < 0.001$, $\eta_p^2 = 0.85$; a reduction of roughly 20-25% when dividing attention). While no main effects were seen across *contexts* ($F(2, 38) = 0.89$, $p = 0.42$) or between the two *target colours* ($F(1, 19) = 0.09$, $p = 0.76$), a significant interaction between *context* and *target colour* was observed ($F(2, 38) = 3.90$, $p = 0.029$, $\eta_p^2 = 0.17$). Post-hoc pairwise comparisons revealed that hit rates for red in the yellow/lime context were higher than in the yellow/orange context ($t(19) = 3.06$, $p = 0.006$, $d = 0.68$). None of the other pairwise comparisons reached significance (all $ts < 2.13$). Likewise, neither of the other two interactions, nor a 3-way interaction were found to be significant (all $Fs < 1$). To summarise these findings, a major determinant for hit rates appears to be whether attention is focused or divided, with a large cost in performance when attention is split between the two targets. This is consistent with as a weakened concentration of the spotlight on the target colour representation, so it is less able to efficiently signal the presence of its target-colour.

Such a cost could stem from the need to re-allocate central, top-down resources to the monitoring of a secondary spotlight (see model in Fig.2). As indicated by the ANOVAs, hit rates were mainly dependent on attentional focus rather than colour context – the increase in red target hit rates for the evidently less distracting lime/yellow context is very minor relative to the overall consistency in performance reduction with the addition of a second target.

False alarm rates (Fig.3a, middle panel) to the colours that were always distractors (i.e. excluding red and green) were analysed using a 3x3x2 repeated measures ANOVA with factors *context (yellow/blue, yellow/orange or yellow/lime), attentional focus (to red, green or both targets)* and *distractor colour from which responses are analysed (fixed: yellow, changing: blue, orange or lime).* Significant differences were found on all three main factors: *context* ($F(2, 38) = 4.36$, $p = .020$, $\eta_p^2 = 0.19$), *attentional focus* ($F(1.56, 29.54) = 16.99$, $p < .001$, $\eta_p^2 = 0.47$) and *distractor colour* ($F(1, 19) = 19.09$, $p < .001$, $\eta_p^2 = 0.50$). While there was no interaction between *attentional focus* and *distractor colour* ($F(2,38) = 1.34$, $p = 0.28$), we observed significant interactions between the factors of *context* and *attentional focus* ($F(2.74, 52.09) = 6.284$, $p < 0.001$, $\eta_p^2 = 0.25$), *context* and *distractor colour* ($F(2,38)=4.83$, $p=0.014$, $\eta p^2=0.20$), as well as a three-way interaction ($F(4, 76) = 3.20$, $p = 0.018$, $\eta_p^2 = 0.14$), qualifying all of the previously reported main effects and interactions.

In line with our context manipulation, the changing distractor (i.e. blue, orange or lime) produced a higher false alarm rate than the fixed distractor (i.e., yellow).Therefore, to decompose the interplay between the three factors in the most interpretable way, we conducted a post-hoc analysis of the highest-order three-way interaction with separate 2-way repeated measures ANOVA (*context* by *attentional focus*) within each level of *distractor colour*. For the false alarms elicited by the yellow distractor, we found only a main effect of *attentional focus* ($F(2,38) = 10.04$, $p < .001$, $\eta_p^2 = 0.35$), with more false alarms when attention had to be divided than when it was focused either on red ($t(19) = 3.68$, $p = .002$, d =

0.83) or green ($t(19) = 3.74$, $p = .001$, $d = 0.84$; no difference between focusing on red or green, $t(19) = 0.47$, $p = 0.64$). Context ($F(2, 38) = 0.79$, $p = .46$) had no effect and there was no interaction ($F(2.80, 53.14) = 1.47$, $p = 0.22$), confirming that the yellow distractor was contextually neutral.

However, for the crucial, context-dependent distractor, we found both a main effect of *attentional focus* ($F(2,38) = 16.22$, $p < .001$, $\eta p^2 = 0.46$), and *context* ($F(2, 38) = 6.19$, $p = .005$, $\eta_p^2 = 0.25$) as well as their interaction ($F(4, 76) = 7.75$, $p < .001$, $\eta_p^2 = 0.29$). Dividing attention between red and green led to robustly higher false alarm rates for the blue distractor when compared to attending red alone (red: $t(19) = 4.77$, $p < .001$, $d = 1.07$; green: $t(19) = 1.85$, $p = .08$), orange compared to attending green alone (green: $t(19) = 4.95$, $p < .001$, $d = 1.07$; red $t(19) = 1.88$, $p = .08$), and lime distractor when compared to attending red alone (red: $t(19) = 5.52$, $p < .001$, $d = 1.24$; green: $t(19) = 1.70$, $p = .11$). Therefore, distraction in divided attention is only increased relative to a single spotlight on the more distal colour (green target for orange distractor; red target for lime distractor). In addition to that, increased false alarms for divided attention to blue distractor relative to focused attention to red target in the supposedly neutral context indicate that in CIELAB, blue is attentionally more proximal to green than to red.

A few other significant differences were observed, consistent with the previously reported results: lime distractors when red was attended generally elicited very few false alarms (fewer than: divided focus blue ($t(19) = 5.94$, $p<.001$, $d = 1.33$; divided focus orange $t(19) = 5.63$, $p <.001$, $d = 1.26$). Orange distractors when green was attended also elicited very few false alarms (fewer than: divided focus lime ($t(19) = 4.49$, $p < .001$, $d = 1.00$; divided focus blue, $t(19) = 5.63$, $p < .001$, $d = 1.26$; green focus blue $t(19) = 3.63$, $p = 0.002$, $d = 0.81$). Orange distractors elicited more false alarms when red as opposed to green was attended ($t(19) = 3.82$, $p = .001$, $d = 0.85$), while blue ($t(19) = 2.63$, $p = 0.017$) and lime

($t(19) = 2.53$, $p = 0.02$) were not as robustly different between the two individual spotlights. Finally, divided focus blue elicited more false alarms than lime when green was attended ($t(19) = 3.69$, $p = 0.002$, $d = 0.85$). This is also consistent with previous evidence that lime is not as distracting when spotlight is on green as might be predicted based on CIELAB distances alone. All other t-tests did not survive correction for multiple comparisons ($ts < 3.46$, $ps > .003$).

As red and green also acted as distractors in one of the attentional conditions per context (i.e., when red was attended, green acted as distractor, and vice versa) a repeated measures ANOVA with factors of *context* (yellow/blue, yellow/orange and yellow/lime) and *distractor* (red, green) was performed to assess any potential differences. All factors were insignificant ($Fs < 1.28$, $ps < 0.29$). This is consistent with their similar efficiency of selection when presented as single targets.

Finally, criteria (Fig.3a, bottom panel) were subjected to a 3x3 repeated measures ANOVA, with factors of *context* (yellow/blue, yellow/orange and yellow/lime) and *attentional focus* (red, green, both). The analysis yielded a significant effect of *attentional focus* ($F(1.518, 28.834) = 5.835$, $p = 0.012$, $\eta_p^2 = 0.286$). The effect of context and the interaction did not reach significance ($Fs < 1$). Post-hoc tests revealed that a more conservative criterion manifested itself in the divided attention condition in comparison to attending to red alone ($t(19) = 2.550$, $p = 0.02$, $d = 0.570$) or green alone ($t(19) = 2.704$, $p = 0.014$, $d = 0.605$). There was no difference between the bias in the attend red alone and attend green alone conditions ($t < 1$). A more conservative bias indicates that an increase in false alarms was not due to a more liberal response criterion. This is consistent with our observation that the main effect of divided attention is a large fall in hit rates when compared to focused attention.

In summary, our behavioural data revealed three key patterns: 1) divided attention led to a reduction of hit rates and an increase in false alarm rates, with the reduction in hit rates being more pronounced, as corroborated by the more conservative response criterion for divided attention; 2) false alarms increased with target-distractor proximity in colour space; 3) the idea that equivalent coordinates in CIELAB space translate to equal attentional selection was only partially supported. While there was no difference between attending red and green in elicited false alarms for yellow distractors, this was note case for blue distractors, which caused more distraction for green targets. Additionally, lime distractors seemed less potent in eliciting false alarms than orange distractors, despite being fully matched to them in CIELAB.

EEG experiment

Behavioural results

Collapsed across all conditions, hit rates were 65% ± 13%; false alarm rates 9% ± 10% and criterion 0.43 ± 0.31 (means and standard deviations; see Figure 3b). Once again this confirms that the task was achievable. In comparison to the behavioural experiment, the decrease in overall hit rates and increase in false alarm rates can be attributed to the addition of flicker. Some participants particularly struggled performing the motion detection task on flickering RDKs, as evidenced by the increase and variability of FA rates. As described in the participant section, 4 observers became unable to perform the task reliably and were removed from the sample.

Rather than affecting performance similarly across conditions, flicker selectively decreases the saliency of motion signals for stimuli at lower temporal rates when compared to stimuli at higher temporal rates (Nakayama & Silverman, 1984), complicating the comparison of behavioural data across flicker frequencies. Finally yet importantly,

behavioural data obtained from the EEG experiment is based on fewer coherent motion events, since their number was reduced to increase periods of attentional monitoring without coherent motion. Put together, behavioural data from the EEG experiment is noisier due to being calculated from fewer events and suffers from a selective reduction of salience of coherent motion signals for colours that flickered at lower frequencies. Still, we performed the same repeated measures ANOVAs and confirmed that the most salient data patterns (high cost in hit rates and a more conservative bias for divided attention; more false alarms elicited by the changing distractors) were the same between experiments.

For the hit rates, the effect of *attentional focus* was again very pronounced ($F(1, 19) = 64.782$, $p < 0.001$, $\eta_p^2 = 0.773$), with a reduction in performance when dividing attention between two colours. Neither the effect of *context* ($F(1, 19) = 1.444$, $p < 0.249$), nor the effect of *target* ($F(1, 19) = 0.026$, $p = 0.874$) reached significance. Additionally, none of the interactions were significant (all Fs < 2.061, all ps > 0.141).

False alarm rates significantly depended on both *attentional focus* ($F(1,19) = 11.870$, $p < 0.001$, $\eta_p^2 = 0.385$) and *distractor type* (lower distraction from yellow than from blue/orange/lime; $F(1, 19) = 24.606$, $p < 0.001$, $\eta_p^2 = 0.564$), but not on *context* ($F(1, 19) = 1.382$, $p = 0.263$). Follow-up tests showed that false alarm rates were higher when attention was divided, as opposed to when it was focused on red ($t(19) = 3.281$, $p = 0.004$, $d = 0734$) or on green ($t(19) = 4.296$, $p < 0.001$, $d = 0.961$). False alarm rates between the conditions where red or green were attended alone did not differ ($t(19) = 1.792$, $p = 0.89$, $d = 0.401$). No significant interactions were observed (all Fs < 2.497, all ps > 0.096).

Furthermore, response criterion also depended on *attentional focus* ($F(2, 38) = 12.706$, $p < 0.001$, $\eta_p^2 = 0.401$). Participants became more conservative when attention was divided as opposed to focused on red alone ($t(19) = 4.343$, $p < 0.001$, $d = 0.971$) or green alone ($t(19) = 4.062$, $p = 0.001$, $d = 0.908$). There was no difference between the criterion

when single colours were attended ($t(19) = 0.201$, $p = 0.842$, $d = 0.045$). Criterion was also not significantly affected by *context* ($F(1, 19) = 1.162$, $p < 0.324$) or an interaction between the two factors ($F(1, 19) = 0.616$, $p = 0.652$).

SSVEP results

SSVEP spectra, topographies and amplitudes are depicted in Figure 4a-b. To investigate how SSVEP amplitudes were influenced by the different conditions of the experiment, a 3x2x2 repeated measures ANOVA was performed on the attentional effect (attended minus unattended SSVEP amplitude; Fig. 4c), with factors *context (yellow/blue, yellow/orange or yellow/lime), attentional focus (to a single target or divided between two targets)* and *target colour from which responses are analysed (red or green).* The factor of *attention* had a very large influence on SSVEP amplitude ($F(1, 19) = 53.550$, $p < 0.001$, $\eta_p^2 = 0.74$) – the attentional increase was reduced when attention was divided between two colours (0.25 ± 0.03 µV) as opposed to when it was focused on a single colour (0.42 ± 0.04 µV). In the behavioural experiment, we had observed a similar pattern in hit rates. Neither the factor of *context* ($F(2, 38) = 2.101$, $p = 0.136$) nor *target colour* ($F(1, 19) = 4.306$, $p = 0.052$) reached significance. However, the interaction between *context* and *target colour* was significant ($F(2, 38) = 4.211$, $p = 0.022$, $\eta_p^2 = 0.18$). Further examination of this interaction revealed that the attentional effect for red in the yellow/lime context was higher when compared to red in the yellow/orange context ($t(19) = 3.841$, $p = 0.001$, $d = 0.859$). Additionally, the attentional effect for red was more pronounced than that for green within the yellow/lime context ($t(19) = 3.363$, $p = 0.003$, $d = 0.752$). No other interaction was significant (all $Fs < 1$, $ps > 0.38$).

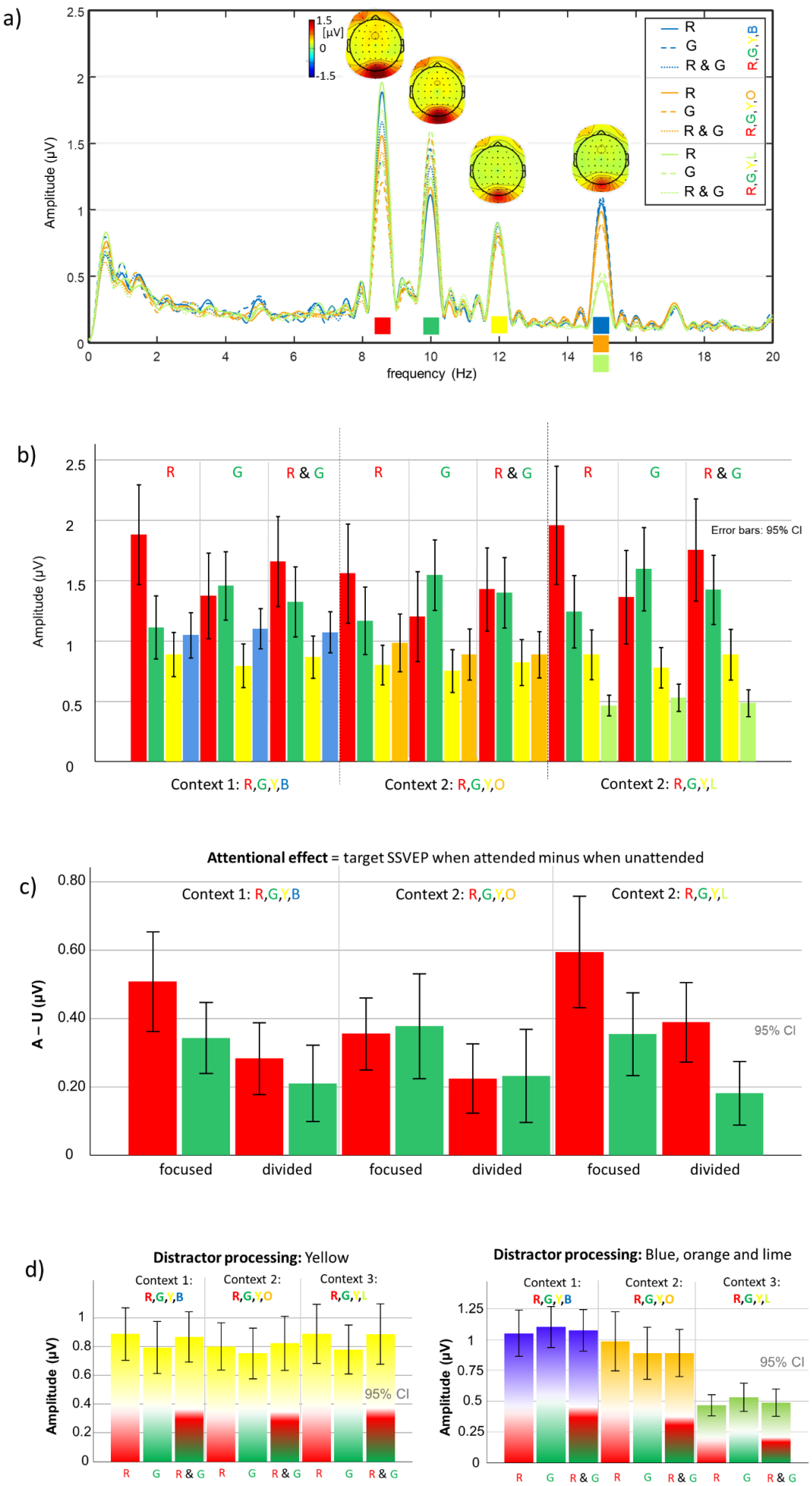
a)
Amplitude (µV)
frequency (Hz)
1.5
[µV]
0
-1.5
R
G
R & G
R,G,Y,B
R,G,Y,O
R,G,Y,L
b)
Amplitude (µV)
Error bars: 95% CI
Context 1: R,G,Y,B
Context 2: R,G,Y,O
Context 2: R,G,Y,L
c)
Attentional effect = target SSVEP when attended minus when unattended
A – U (µV)
95% CI
focused
divided
d)
Distractor processing: Yellow
Distractor processing: Blue, orange and lime
Context 1: R,G,Y,B
Context 2: R,G,Y,O
Context 3: R,G,Y,L
Amplitude (µV)
95% CI

Figure 4. ***SSVEP results****. A) Spectra and topographies. Full lines depict amplitudes elicited when red was the target colour, dashed lines depict amplitudes elicited when green was the target colour and dotted lines depict amplitudes when attention was divided between red and green. The colour of the line depicts the context, which in addition to red, green and yellow included either blue, orange or lime. b) Bar graph of amplitudes, depicting more clearly the SSVEP amplitudes at flicker frequency for each of the stimulus colours. c) Bar graph of attentional effects calculated from SSVEP amplitudes elicited by green and red targets. Unattended amplitude for the red colour is taken from the 'attend green' condition, and vice versa. d) Bar graphs of distractor-driven amplitudes, with the yellow distractor on the left and the changing distractor (blue, orange or lime, depending on the context) on the right. Error bars: 95% between-subject CIs.*

To investigate how distractors were processed between contexts, we first focused on the SSVEP amplitude elicited by yellow, which was the distractor that was constantly present. A 3x3 repeated measures ANOVA with factors of *context (yellow/blue, yellow/orange or yellow/lime),* and *attentional focus (to red, green or split)* was conducted (see Figure 4d). We found main effects of *context* ($F(2, 38) = 5.15$, $p = .011$, $\eta_p^2 = 0.21$) and *attentional focus* ($F(2, 38) = 15.42$, $p<.001$, $\eta_p^2 = 0.45$), without an interaction ($F(4, 76) = 0.57$, $p = .68$). Amplitude for yellow was lower in the orange context compared to lime ($t(19) = 3.105$, $p = .006$, $d = 0.694$; the other differences were not significant, blue vs. lime $t(19) = 0.100$, $p = 0.921$; blue vs. orange, $t(19) = 2.478$, $p = 0.024$). In addition, amplitude was lower when attention was focused on green, compared to when attention was divided between both red and green ($t(19) = 5.600$, $p < .001$, $d = 1.252$) or when focused on red ($t(19) = 4.882$, $p <.001$, $d = 1.092$; red vs. divided attention not significantly different, $t(19) = 0.016$, $p = 0.988$).

We also conducted a repeated measures ANOVA with factor *attentional focus (red, green or split)* for each of the changeable distractor colours to reveal whether their neural processing was affected by the target colour(s). For blue ($F(2, 38) = 1.33$, $p = .27$) and lime ($F(2, 38) = 2.42$, $p = .103$) we found no significant differences. For orange ($F(2, 38) = 5.31$, $p = .009$, $\eta p^2 = .22$) amplitude was higher when attending red compared to attending green ($t(19) = 2.853$, $p = .011$, $d = 0.638$). The other differences were not as robust (red vs. dividing attention between red and green ($t(19) = 2.622$, $p = .0183$, $d = 0.586$; green vs. dividing attention between red and green, $t(19) = 0.001$, $p = 0.99$).

In a final analysis, we evaluated if attentional increases at the neural level follow a simple resource allocation model. If this were the case, attentional modulation in divided attention conditions should be half of its magnitude when only single colours are attended (Adamian & Andersen, 2022; Adamian, Slaustaite, & Andersen, 2019; Andersen, Müller & Hillyard, 2009). Accordingly, target SSVEP amplitudes in divided attention conditions would equal the average of attended and unattended conditions (i.e. the attend red and attend green conditions). Alternatively, if these were implemented independently for each spotlight, akin to selection of feature values from different dimensions (Adamian et al., 2019; Andersen et al., 2015), then attentional modulation in the divided attention condition would be as large as in the attend single colour conditions. Figure 5 depicts predictions based on simple resource allocation (i.e. half the attentional increase when splitting the spotlight of attention), which generally seem to fit the data, only slightly underestimating the actual SSVEP amplitudes ($-2.650 < t < -0.135$; $0.894 < p < 0.016$; the only robust deviation from predictions being for red in the yellow/lime context).

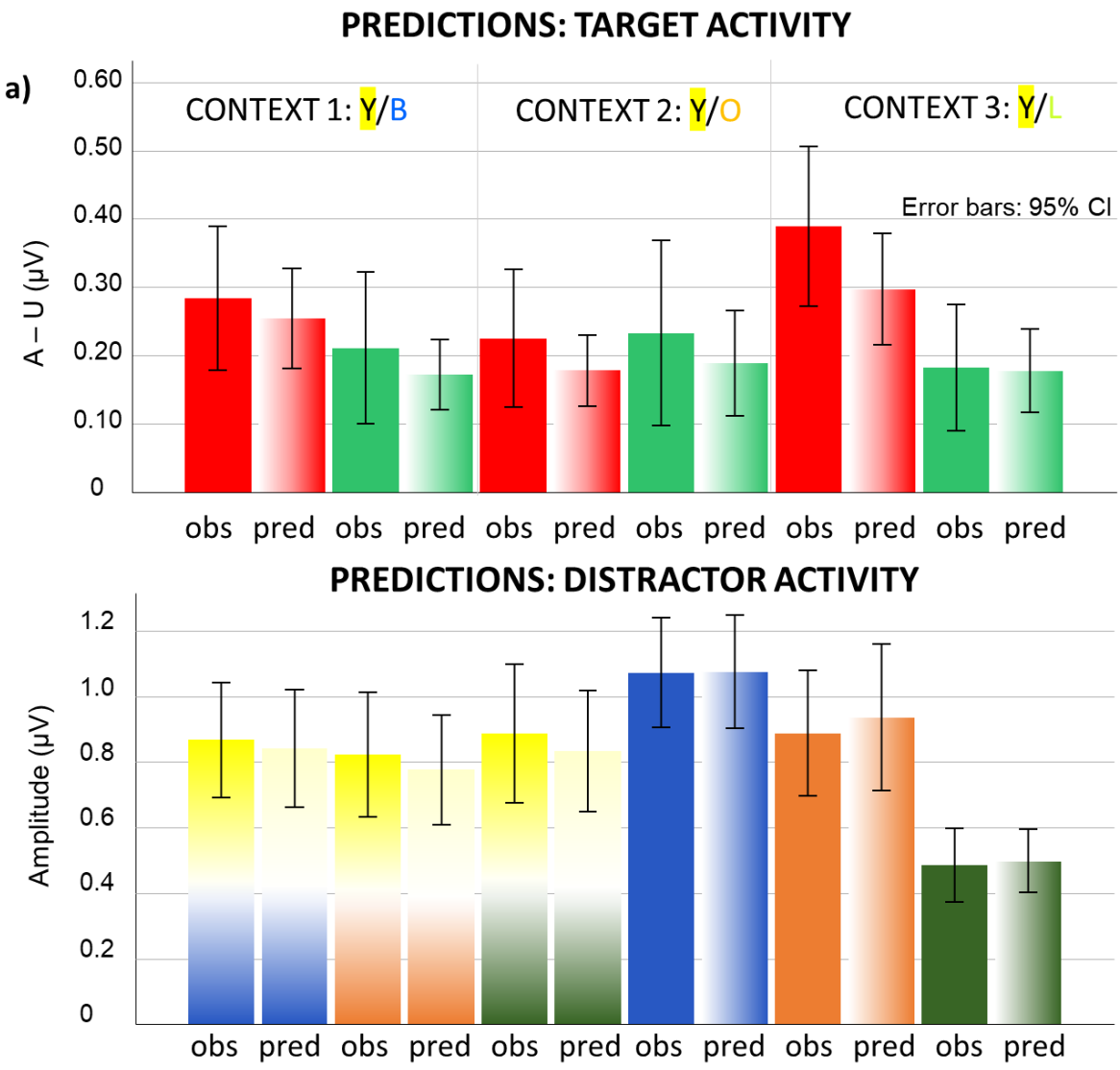

Figure 5. Comparisons of target (upper panel) and distractor-driven (lower panel) neural activity with predictions derived from a simple resource allocation model. *Observed neural activity (abbreviated to 'obs') is plotted next to predicted neural activity (abbrev.: 'pred'). Simple resource allocation would predict that observed neural activity when splitting the spotlight of attention across two targets should equal to half of the attentional increase in the single-target condition. This reflects a single attentional resource that is evenly divided. If distractor interference is combined across the two spotlights in a similar manner, than activity observed from the divided attention condition should equal an average of activities elicited in single-target conditions. This simple model approximates the data patterns fairly*

well, although it consistently slightly underestimates the target-driven SSVEP amplitudes. The main deviation from the model is red in the yellow/lime context – where the divided attentional resources may be larger due to potential top-down influences of relational grouping of all distractors containing 'yellow', thus releasing the targets from competitive pressures (see Discussion).

As indicated by the ANOVAs, distractor amplitudes are affected by attentional focus: yellow-driven amplitude is lower when attention is focused on green while orange-driven amplitude is higher when attention is focused on red. If distractor effects are independently combined across the two spotlights, then the amplitude for e.g. yellow when attention is divided between red and green should be half of yellow-driven amplitudes in single-spotlight conditions. This is indeed the case for all colours ($-1.745 < t < 0.443$, $0.097 < p < 0.663$; see Fig. 5b).

Discussion

To investigate whether attentional selection of colour can be conceived as a spotlight that highlights areas of the multidimensional colour space, we designed an experiment that manipulated both the number of colour targets (one or two) and the proximity of distractors to the targets (neutral or closer to one of the targets). In a sustained multi-coloured RDK motion detection task, we placed red and green targets in one of three contexts: i) a neutral context with intermediate distractors, falling between the two target hues in CIELAB space (blue and yellow); ii) a context with one distractor closer to red (orange and yellow); iii) a context with one distractor closer to green (lime and yellow). In the behavioural experiment, we found that hit rates were overwhelmingly dependent on whether attention was focused or divided, implying that concurrent application of two spotlights to two colours was possible,

but came at a significant cost to attentional efficiency in target selection. On the other hand, false alarms were more strongly affected by context: blue, orange and lime distractors affected the performance differentially, unlike the universally present yellow distractors. Meanwhile, SSVEP data was consistent with a combination of two independently acting spotlights whose efficiency was halved with divided attention. Representational proximity between targets and distractors had a minor effect at best. From this, we conclude that concurrent attention to two categorically distinct colours is more limited by a central, resource-related bottleneck rather than by a local, perceptual-level bottleneck.

The spotlight metaphor, which is prominent in spatial attention research, fits with the corresponding patterns of behaviour and neural activity remarkably well. Selection of multiple feature values from the same dimension seems highly consistent between colour (Andersen et al., 2013) and space (Adamian & Andersen, 2022; Adamian et al., 2019; Toffanin, de Jong, Johnson, & Martens, 2009), with reduced attentional modulation in divided attention conditions as proposed by the original Zoom lens model (Eriksen & St. James, 1986) and processing of distractors modulated by target-distractor proximity in the feature-dimension on which selection is based (Martinez-Trujillo & Treue, 2004; Martinovic et al., 2018; Treue & Martinez-Trujillo, 1999). At the same time, attentional selection of feature values from different dimensions, such as colour and orientation (Andersen et al., 2015) or space and colour (Adamian et al., 2019) is strikingly independent. For example, attentional co-selection of red and green is associated with costs, whereas co-selection of red and horizontal is not. Put together, this strongly implies that attentional modulation of signals in biological systems is implemented using the same type of domain-general mechanisms, which operate independently for each dimension.

As predicted, we found higher rates of responses to distractors in contexts that put them closer to one colour, e.g. orange elicits more false alarms when the target is red and

lime elicits more false alarms when the target is green. However, contrary to our predictions, this did not occur evenly across our contexts, which were presumed to be either neutral (blue), closer to red (orange) or closer to green (lime). Blue was found to elicit more false alarms when the target was green, while the overall number of false alarms was the lowest in the yellow/lime context. CIELAB is perceptually uniform, derived from data on time-unlimited discriminations of suprathreshold colour differences. However, this does not guarantee in any way its uniformity in terms of attentional effects. Unlike simple colour discrimination, attention to colour as observed in visual search for colour targets is influenced by categorical status (Found & Muller, 1996), which can be used to set attentional templates based on an element's relative position in relation to the other colours in the display (e.g. 'redder than' or 'yellower than'; Becker, 2010). We observed higher levels of distractor interference, both behaviourally and neurally, for the orange colour as compared to the lime colour. This asymmetry is not consistent with positions of our stimulus colours in CIELAB nor with their positions in relation to unique hues (see Fig. 1), but is consistent with categorical labelling data, which indicates a larger overlap between orange and red (Malkoc, Kay, & Webster, 2005, Fig. 1). The fact that CIELAB may be perceptually but not attentionally uniform poses problems for studies that probe multiple locations in CIELAB but subsequently collapse the data across hues (e.g. Stormer & Alvarez, 2014).

In a sustained task such as ours, proximity to categorical best-exemplars may act directly, by facilitating the efficient setting and maintenance of attentional templates (Bae, Olkkonen, Allred, & Flombaum, 2015), or indirectly, by facilitating grouping of more similar hues together, be they targets or distractors (Matera et al., 2020; Oxner et al., accepted). Namely, the orange distractor is more proximal to red than to yellow, leading to a spread of activation in accordance with the feature similarity gain model (Martinez-Trujillo & Treue, 2004). This makes it more difficult to allocate top-down resources (i.e. to successfully bias

competition) towards the red target whilst ignoring orange. If the 'yellowness' of the lime distractor can be successfully used to group it together with yellow and away from green, this would make it easier to bias competition towards the green target. Grouping of local motion signals by colour appears to precede global motion processing and is under attentional control (Martinovic, Meyer, Muller, & Wuerger, 2009; Wuerger, Ruppertsberg, Malek, Bertamini, & Martinovic, 2011). If colour similarity increases the grouping of colours in the RDK, this would create predicted costs when they need to be selected or ignored independently (e.g. red/orange) but also produce unexpected benefits when they need to be ignored together (e.g. yellow/lime). In fact, the special status of colour as an extremely salient feature dimension in terms of attention (see Found & Muller, 1996) is at least partly derived by our ability to maintain and use multiple templates in short-term memory that are based on a colour's categorical status, mediated through ease of verbal labelling (Forsberg, Johnson, & Logie, 2019). As discussed in a recent review by Liesefeld and Mueller (2019), this multidimensionality of colour is likely to have important repercussions for colour-based attentional selection. Based on our results, unique hue axes may represent important determinants of colour-based attention on account of being an effective link between relational colour appearance (e.g. 'more yellow than'; Becker, 2010) on one hand, and categorical colour representativeness, on the other hand. Indeed, Liesefeld and Mueller (2019) speculate that red-green and blue-yellow axes may be fundamental for colour selection, but they do not state the nature of these axes – e.g. whether they would be determined by cone-opponent or colour-opponent inputs. If top-down colour selection is a product of modulation of bottom-up cone-opponent activity by higher-order representations such as colour categories or relative unique hue content (e.g. yellowness, redness, greenness or blueness; see Matera et al., 2020) the fact that behavioural and neural effects of colour-based attention are captured well by our spotlight model bodes well for future studies that

will aim to disentangle these contributions using feature-based attention paradigms such as ours.

Returning to the highly congruent effects observed in behavioural and neural data, the ~20-25% cost in hit rates for divided attention corresponded to a 50% reduction in the attentional effect that was well predicted by a simple averaging of the amplitudes elicited by red and green in the two focused attention conditions. Certain correspondences were also found in false alarm rates and reductions in target-elicited SSVEPs due to the presence of proximal distractors: in the visual cortices both orange and lime interfered with the processing of red and green targets. However, we do not observe an SSVEP reduction in the blue context. Thus, while the neural markers of attention follow more closely a symmetrical effect of distractors on target processing which is well captured by distances in CIELAB space, the behavioural data is more in line with an additional influence of higher-level processes, such as grouping by colour and colour categorisation.

In conclusion, we have shown that divided attention to colour can be predicted from single colour selection. Colour distances in CIELAB space only partially account for our results, with blue producing more false alarms than yellow and orange more than lime, despite equivalent CIELAB coordinates. The findings of our study pave the way for a more refined exploration of the relations between categorical status, colour content (e.g., as identified by hue scaling) and perceptual differences. Should full understanding of these relations be obtained, it will be possible to quantify an attentional colour space, which could be used to predict the ease with which colours can be selected together or filtered out as distractors.

Open science

Raw behavioural and averaged EEG data is publicly available on Open Science Framework (OSF): https://osf.io/2kjsx/

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