Vision Research 95 (2014) 36–42

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Saliency interactions between the 'L-M' and 'S' cardinal colour directions

Frederick A.A. Kingdom [a,*], Natacha Kardous [a], Laura Curran [a], Elena Gheorghiu [b], Jason Bell [c,d]

[a] McGill Vision Research, Department of Ophthalmology, 687 Pine Av. W., Rm. H4-14, Montreal, Quebec H3A 1A1, Canada
[b] Department of Psychology, University of Stirling, Stirling FK9 4LA, United Kingdom
[c] Research School of Psychology, The Australian National University, Room 123, Building 39, Canberra, ACT 0200, Australia
[d] School of Psychology, University of Western Australia, Perth, WA 6009, Australia

ARTICLE INFO

Article history:
Received 28 August 2013
Received in revised form 9 December 2013
Available online 18 December 2013

Keywords:
Colour vision
Saliency interactions
Cardinal colours

ABSTRACT

Two sub-systems characterize the early stages of human colour vision, the 'L-M' system that differences L and M cone signals and the 'S' system that differences S cone signals from the sum of L and M cone signals. How do they interact at suprathreshold contrast levels? To address this question we employed the method used by Kingdom et al. (2010) to study suprathreshold interactions between luminance and colour contrast. The stimulus employed in one condition was similar to that used by Regan and Mollon (1997) for studying the relative 'organizing power' of the two sub-systems, and consisted of obliquely-oriented red-cyan (to isolate the L-M sub-system) and violet-chartreuse (to isolate the S sub-system) stripes within a lattice of circles. In our experiment there were two conditions, (1) the Separated condition, in which the L-M and S modulations were of opposite orientation and presented separately as a forced-choice pair, and (2) the Combined condition, in which the L-M and S modulations were added. In the Separated condition the task was to indicate the stimulus with the more salient orientation structure, whereas in the Combined condition the task was to indicate the orientation that was more salient. Psychometric functions were used to estimate the ratio of L-M to S contrast at the 'balance-point' i.e. point-of-subjective-equality (PSE) in both conditions. We found that across 20 subjects an average of 8% more S than L-M contrast was needed to achieve a PSE in the Combined compared to Separated condition. We consider possible reasons for this PSE difference and conclude that it is either due to an early-stage interaction between the S and L-M sub-systems, or to a later stage in which new colours that arise from their combination are selectively grouped.

1. Introduction

Two cone-opponent sub-systems characterize the early stages of colour vision. One sub-system, termed here 'L-M', differences the L (long wavelength-sensitive) and M (middle-wavelength-sensitive) cone signals. The other, termed here 'S', differences the S (short-wavelength-sensitive) with the sum of L and M cone signals. To isolate the two sub-systems one employs stimuli defined along the cardinal axes of the isoluminant plane of the MB (MacLeod-Boynton), or closely related DKL (Derrington, Krauskopf, and Lennie) colour space (Cole, Hine, & McIlhagga, 1993; Derrington, Krauskopf, & Lennie, 1984; Krauskopf, Williams, & Heeley, 1982; MacLeod & Boynton, 1979; Norlander & Koenderink, 1983; Sankeralli & Mullen, 1997; Stromeyer, Cole, & Kronauer, 1985). As shown in Fig. 1 the cardinal axes vary respectively from red to cyan on the one hand and violet to chartreuse on the other.

Studies investigating whether the cone-opponent sub-systems function independently at contrast detection threshold have produced mixed results (e.g. Mullen & Sankeralli, 1999, versus Chen, Foley, & Brainard, 2000a, 2000b). How do the two sub-systems interact when processing suprathreshold colours to which they are both sensitive? In the present study we approach this question by measuring the relative saliencies of stimuli that activate the two sub-systems, both when the stimuli are presented separately and when combined. If the two sub-systems interact, we should expect the relative saliences to be different in the combined compared to separate conditions.

Regan and Mollon (1997; see also Mollon, 1995, chap. 5) compared the 'organizing power' of the two sub-systems using a stimulus similar to that shown in Fig. 1c. In Fig. 1c, opposite oblique orientations of L-M and S modulations have been added in a lattice of circles. In Regan and Mollon's experiment, subjects were required on each trial to indicate whether the dominant perceptual organization was left or right oblique. A staircase procedure varied the relative contrasts of the two modulations to establish the 'balance point', i.e. point-of-subjective-equality (PSE). Regan and Mollon found that the balance point depended on the spatial separation of the circles in the lattice, and suggested two reasons for this: the different spatial resolutions of the two sub-systems

* Corresponding author.
E-mail address: fred.kingdom@mcgill.ca (F.A.A. Kingdom).

0042-6989/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.visres.2013.12.004

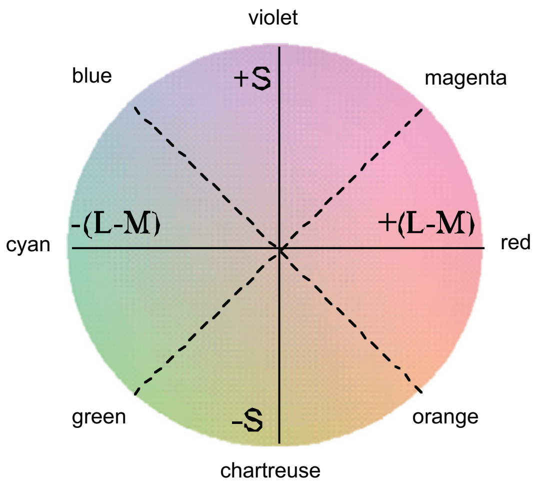

Fig. 1. Isoluminant plane of the DKL colour space showing both the cardinal (continuous lines) and intermediate (dashed lines) axes.

and the chromatic aberration of the eye. They also compared normal trichromats with 'red-green' anomalous trichromats, and as expected found that the balance-point shifted in favour of the S component for the latter. This method of arranging a competition between two attributes within the same stimulus resonates with the approach developed by Papathomas and Gorea (1988) for studying the relative contributions of two attributes (e.g. colour and luminance) to motion perception. In their study, subjects varied the relative contrasts of the two components until a motion direction null was obtained [see also Gorea and Papathomas (1991) and Papathomas et al. (1995) for extensions of the paradigm].

One arguable limitation of Regan and Mollon's method is that it does not allow one to distinguish between an *interaction* between two attributes as opposed to their *independent contribution* when combined. To this end, we have employed a modification of their method devised by Kingdom et al. (2010) for studying the interaction between suprathreshold colour and luminance contrasts [and see the brief report by Schofield and Kingdom (2012) for the method applied to interactions between colour, luminance and texture]. The key feature of the method is that it directly compares the results from two experimental conditions, termed 'Separated' and 'Combined', which are illustrated in Fig. 2. In the Separated condition, shown in Figs. 2a and b, the L-M and S patterns are presented *separately* as a two-interval forced-choice pair with various relative contrasts and the subject is required on each trial to select the pattern with the more salient orientation structure. A PSE is estimated from the resulting psychometric function. In the Combined condition, shown in Fig. 2c, opposite oblique modulations of L-M and S are added in the lattice (as in Regan and Mollon), and the subject's task is to decide on each trial whether the dominant orientation is

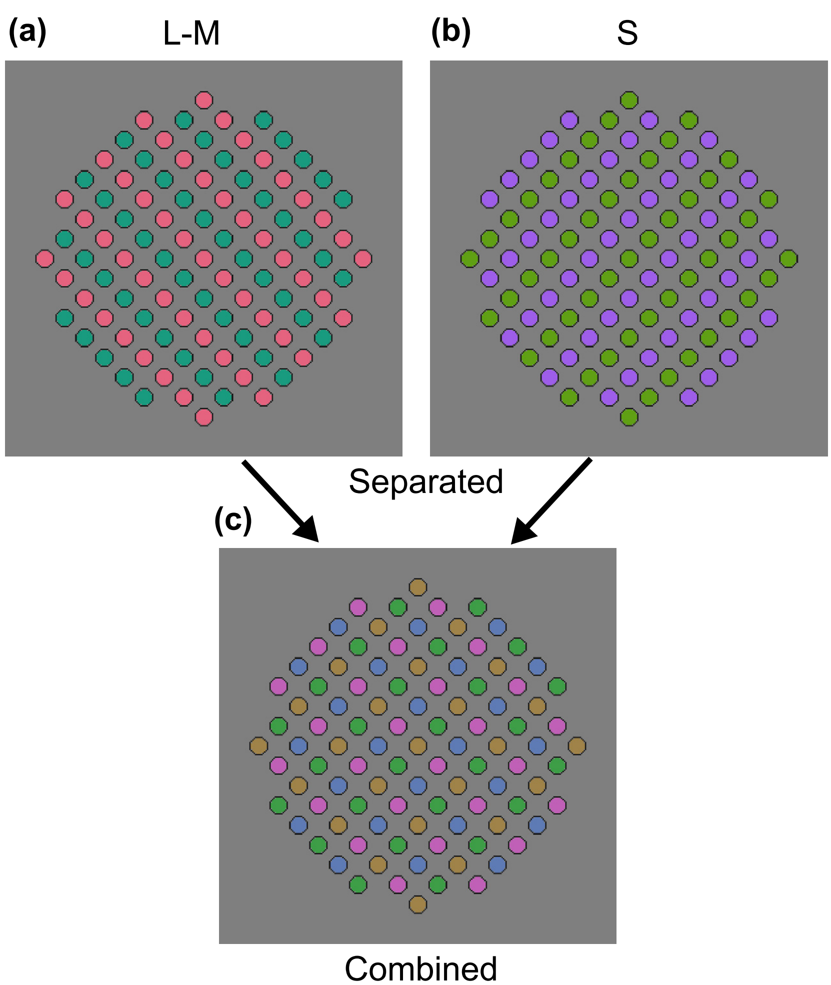

Fig. 2. Stimuli used in the experiments. The upper two lattice patterns are defined by obliquely-oriented modulations along the L-M and S axes, as shown. These patterns are used in the Separated condition. In the bottom stimulus the two upper lattice patterns are added to produce the Combined condition.

left- or right-oblique. The same set of contrasts is used in the Combined as in the Separated condition, and the PSE, this time defined as the relative S to L-M contrasts that make the left- and right-oblique orientations equally salient, is estimated from the psychometric function. The question we ask is whether the PSEs are different for the Separated and Combined conditions. If they are, this indicates that there must be an interaction between the S and L-M stimuli when the two are combined. One can think of the Separated condition as a baseline, or normalizing PSE, against which the Combined PSE is compared.

Readers may wonder why the circles in our lattice patterns are surrounded by thin black rings. We found that without the rings the colours tend to spread out from the circles perceptually to form thin semi-transparent veils. Although the question of how colours interact in perceptual transparency is an important one, it is not the question we wish to address here. Rather, we want to know how the L-M and S modulations interact when their component colours are added in clearly demarcated patches, and the black rings help create the desired percept.

It is noteworthy that subjects found both tasks easy. One might suppose that the Separated condition is difficult because subjects are required to compare the saliences of colours defined along orthogonal colour directions. However, Switkes and Crognale (1999) and Switkes (2008) reported that subjects were able to reliably and lawfully match the saliencies of suprathreshold gratings defined along different directions of colour space, so the ease with which our subjects perform this task should not come as a surprise.

2. Methods

2.1. Subjects

Twenty subjects participated. FK, JB, EG and LC were authors, while the remaining subjects were volunteers who were naïve as to the purpose of the experiment. All observers had normal or corrected-to-normal visual acuity and normal colour vision as tested using the Ishihara plates.

2.2. Stimuli – generation and display

The stimuli were generated by a VISAGE graphics card (Cambridge Research Systems) and displayed on a Sony Trinitron F500 flat-screen monitor. The R (red), G (green) and B (blue) gun outputs of the monitor were gamma-corrected after calibration with an Optical photometer (Cambridge Research Systems). The spectral emission functions of the R, G and B phosphors were measured using a PR 640 spectral radiometer (Photo Research) with the monitor screen filled with red, green or blue at maximum luminance. The CIE coordinates of the monitor phosphors were R: $x = 0.624$, $y = 0.341$; G: $x = 0.293$, $y = 0.609$; B: $x = 0.148$, $y = 0.075$.

In both the Separated and Combined conditions (see below) the two component patterns were generated on separate pages of the VISAGE's video memory along with their own look-up-tables (LUTs). During stimulus presentation the two video pages (and corresponding LUTs) were alternated at the monitor frame rate of 120 Hz, resulting in a stimulus refresh rate of 60 Hz. For the Separated condition each component frame alternated with a blank screen filled with the background grey (see below), whereas in the Combined condition the two component frames alternated with each other. The frame alternation ensured that in the Combined condition there were no within-frame interactions between the components, and hence any measured interactions were perceptual in origin. The method of frame alternation results in contrasts that are half of those specified in the stimulus generation program, and it is the correct, 'halved' values that are reported here.

2.3. Stimuli – lattice patterns

Example stimuli are shown in Fig. 2. The diameter of the pattern was 3.7 deg at the viewing distance of 110 cm. Therefore the outer edges of the stimuli were 1.85 deg in eccentricity, which is within the para-foveal range (<2 deg). There were 11 circles along the oblique diameter and 9 circles along the horizontal and vertical diameters. The circles were arranged such that nearest neighbours lay along oblique axes. Each circle had a diameter of 0.197 deg. The centre-to-centre separation between circles was 0.347 deg along the oblique axis, and 0.49 deg along the horizontal and vertical axes. All circles were ringed by a 1 pixel-wide (0.96 arcmin) black line.

2.4. Stimuli – colours

Each component modulation comprised two colours that straddled the midpoint of an axis defined in the DKL colour space. The isoluminant plane of the DKL colour space consists of two major, or cardinal axes, with points defined by combinations of long-wavelength-sensitive (L), middle-wavelength-sensitive (M) and short-wavelength-sensitive (S) cone *contrasts*. The three cone contrasts are defined as: $L_c = \Delta L/L_b$, $M_c = \Delta M/M_b$ and $S_c = \Delta S/S_b$ (Cole, Hine, & McIlhagga, 1993; Norlander & Koenderink, 1983; Sankeralli & Mullen, 1997; Stromeyer, Cole, & Kronauer, 1985). The denominator in each cone-contrast term refers to the background cone excitation. The background was a mid-grey colour with CIE chromaticity $x = 0.282$ and $y = 0.311$, and luminance 40 cd/m^2. The numerator in each cone contrast term represents the difference in cone excitation between the circle test colour and the background. The LMS cone excitations assigned to each circle and background were converted to RGB phosphor intensities using the cone spectral sensitivity functions provided by Smith and Pokorny (1975) and the measured RGB spectral functions of the monitor.

The two component patterns were defined along the two cardinal axes of the DKL colour space Fig. 1. The term 'cardinal' implies that the colours uniquely stimulate two of the three post-receptoral mechanisms. The relative cone contrast inputs to the three post-receptoral mechanisms have been estimated to be as follows: $kL_c + M_c$ to the luminance (LUM) mechanism, $L_c - M_c$ to the mechanism that differences L and M cone-contrasts, and $S_c - (L_c + M_c)/2$ to the mechanism that differences S from the sum of L and M cone-contrasts (Cole, Hine, & McIlhagga, 1993; Sankeralli & Mullen, 1997; Stromeyer, Cole, & Kronauer, 1985). The parameter k determines the relative weightings of the L and M cone-contrast inputs to the luminance mechanism, varies between observers, and was established for each subject (see below). In order to *isolate* the two cardinal mechanisms the stimuli must be constructed such that the L-M stimulus does not activate either the LUM or the S mechanism, nor the S stimulus either the LUM or L-M mechanisms, nor the LUM stimulus either the S or L-M mechanism. Kingdom, Rangwala, and Hammamji (2005) used the following combinations of L_c, M_c and S_c to achieve this:

$$\text{'L-M'} = L_c - kM_c + S_c(1-k)/2 \tag{1a}$$

$$\text{'S'} = S_c \tag{1b}$$

The measures of contrast were calculated as follows: for L-M, the difference between L_c and M_c; for S, simply S_c.

2.5. Procedure – measurement of isoluminance

Because of inter-subject variation in the relative weightings of the L and M cones that feed the luminance mechanism, it was necessary to ensure that the colours combining L and M cone modulations were isoluminant. We used the criterion of minimum perceived motion. A 0.025 contrast, 0.5 cpd L-M (red-cyan) sinusoidal grating was set to drift at about 1.0 Hz. Subjects pressed a key to add or subtract luminance (L+M) contrast to the grating until the perceived motion was at a minimum. Each subject made between 20 and 30 settings. The average amount of luminance contrast added (or subtracted) was used to calculate the parameter k in Eq. (1b), which is the ratio of L_c to M_c in the putative luminance mechanism. Across subjects the values of k averaged 0.99 with a standard deviation of 0.46.

Although S cones have a negligible input to the luminance mechanism (Eskew, McLellan, & Giulianini, 1999), there is always the possibility of calibration error with S stimuli, so for 16 of the 20 subjects we also measured the isoluminant point for a drifting 0.25 contrast S (violet-chartreuse) grating with the same spatio-temporal parameters as that used for the L-M stimulus. The ratio of L+M to S contrast needed to make the S stimuli isoluminant was on average 0.07 with a standard deviation of 0.014. The setting was not obtained for four of the subjects (SM, JB, EG and LC), and these subjects were presented instead with the S stimuli at photometric isoluminance. In order to ensure that the results were not unduly tainted by any luminance artifacts in these subjects' S stimuli, statistical analyses were conducted both with and without the data from these subjects.

2.6. Procedure – Separated condition

For this condition the two components were presented separately on each trial using a two-interval-forced-choice (2IFC) procedure. An example pair of components is shown in Figs. 2a and b. The task for the subject was to indicate by a key press the interval containing the more salient orientation structure. Each stimulus was presented for 500 ms with an inter-stimulus interval of 500 ms. Trials were initiated by the previous key press, with an interval of 500 ms before the onset of the first stimulus.

Component contrasts were 8 logarithmically-spaced values with a given range and geometric mean. The ratios were chosen such that the geometric mean contrast ratio of the two components was a constant. Thus if the contrasts were indexed a1 to a8 for one component and b1 to b8 for the other, the pairings would be a1 & b8; a2 & b7; a3 & b6; a4 & b5; a5 & b4; a6 & b3; a7 & b2; a8 & b1. The contrasts were selected on the basis of pilot data to ensure that the proportion of responses ranged approximately from '0' to '1'. The range of S and L-M contrasts employed for each subject are shown in Table 1 in the Appendix, together with the range of the (log) ratios of S to L-M contrasts used to define the stimuli. During each session 8 ratios of the two component contrasts were presented in random order, with 20 trials per ratio, making a total of 160 trials per session. There were 3–4 sessions making a total of 480–640 trials per psychometric function.

2.7. Procedure – Combined condition

For this condition the two components were added as in Fig. 2c. As stated above, the two components were presented on alternate video frames to minimize any physical interaction. The same set of contrasts and contrast ratios were employed as in the Separated condition. On each trial the stimulus was presented for 500 ms and a single key press indicated the orientation, left- or right-oblique, that was more salient. Following a response there was a 500 ms inter-trial-interval before the next stimulus was presented. As with the Separated condition there were 160 trials per session, and 3–4 sessions. Separated and Combined sessions were presented in random order.

2.8. Data analysis

Psychometric functions were fitted and analyzed using the Palamedes toolbox (Prins & Kingdom, 2009). The data were fitted with the logistic function

$$F_L(x;\alpha,\beta) = \frac{1}{1+\exp(-\beta(x-\alpha))} \tag{2}$$

where x is the log (logarithm) ratio of component contrasts, α the PSE defined as the ratio producing a proportion of 0.5 responses, and β the slope of the function. The fitting procedure used a maximum-likelihood criterion and the errors on the PSE and slope parameters were estimated by parametric bootstrap analysis.

3. Results

Fig. 3 shows example psychometric functions (PFs) from four of the naïve observers. Each plot shows the proportion of trials in which the subject chose the S component as the more salient, as a function of the logarithm of the ratio of S to L-M contrasts, for both Separated (circles) and Combined (squares) conditions. Best fitting logistic functions are the continuous lines in green and indigo. The PSE was calculated as the log contrast ratio at which the S-contrast defined direction was chosen as more salient 0.5 of the times. The figure shows that there were differences between the two conditions in both PSEs and slopes.

Fig. 4 shows the PSE estimates for all subjects, with standard errors estimated from bootstrap analysis. Of the 20 subjects, 15 show a higher PSE value for the Combined compared to Separated condition. The mean values of the Combined and Separated conditions are 0.755 and 0.720 respectively, and a two-tailed within-subject t-test reveals that the difference is significant at the $p < 0.01$ level [$t(19) = 3.034$; $p = 0.0068$]. As stated in Section 2 four subjects were presented with S stimuli at photometric not behavioural isoluminance, and if we remove these four subjects from the analysis the mean values are 0.767 and 0.721 respectively, a difference with a significance level of $p < 0.001$ [($t(15) = 4.141$; $p = 0.00087$)]. The difference between the Combined and Separated PSEs means that on average, 8% more S contrast was required to balance the L-M contrast in the Combined compared to Separated condition (11% if one removes the four photometric-isoluminant-S subjects). The Separated and Combined PSEs were fairly well correlated within subjects (Pearson's $r = 0.829$; $p < 0.0001$).

The slopes of the psychometric functions were also different, as can be seen in the individual psychometric functions in Fig. 3 and the slope estimates for all subjects in Fig. 5. The mean values of the Combined and Separated condition slopes across all 20 subjects are 6.18 and 10.11 respectively, and a two-tailed within-subject t-test reveals that the difference is significant at the $p < 0.0005$ level [$t(19) = 4.768$; $p = 0.00013$]. The Combined and Separated slopes were significantly correlated ($r = 0.61$; $p < 0.005$). Note that both sets of slopes were normally distributed as tested by the Jarque–Bera test for normality ($p < 0.05$).

4. Discussion

After averaging the results of the main experiment across subjects and colour direction, the difference in PSE between the Separated and Combined conditions is 0.035 log units, corresponding to an 8% difference. Although significant, this difference is small. The direction of the PSE difference shows that slightly more S contrast relative to L-M contrast is needed to balance the two modulations when combined. The steeper slopes of the Separated compared to Combined psychometric functions show that the judgments in the former condition were more precise.

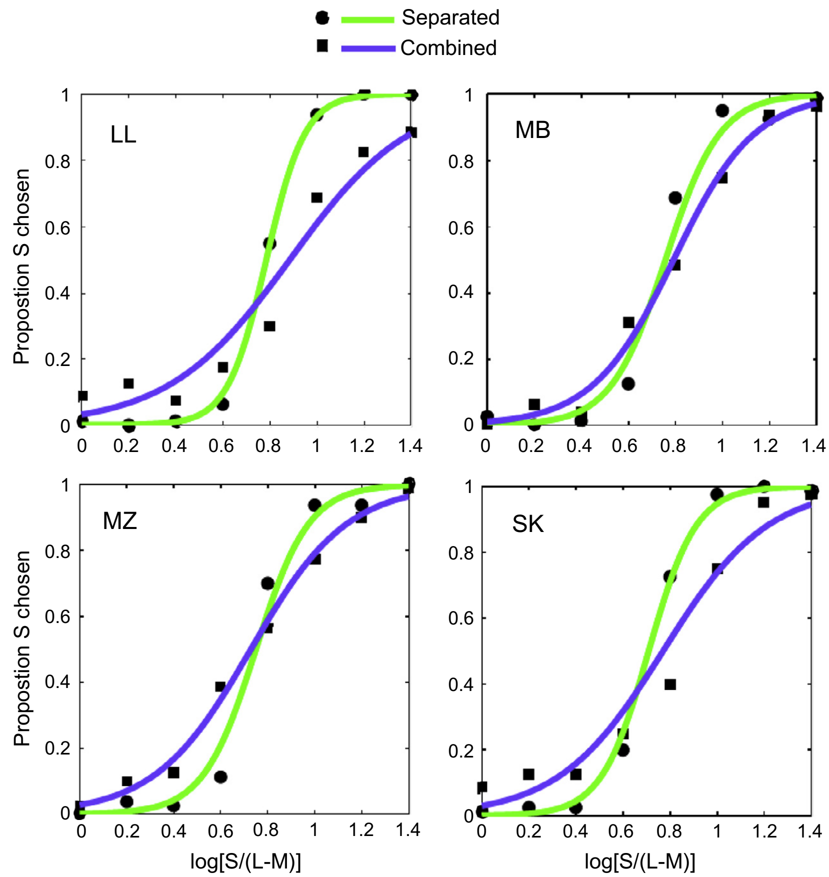

Fig. 3. Example psychometric functions for four naïve observers, for both Separated (circles) and Combined (squares) conditions. The proportion of trials in which the S pattern was chosen as more salient is plotted as a function of the logarithm of the ratio of S to L-M contrasts. Continuous lines are best fitting logistic functions (green for Separated, indigo for Combined). Points-of-subjective-equality (PSEs) are calculated as the values on the abscissa corresponding to the proportion of 0.5 on the ordinate.

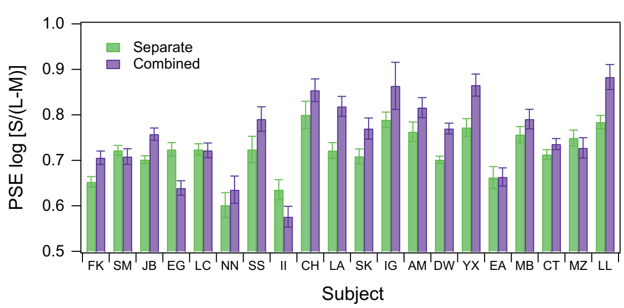

Fig. 4. Points-of-subjective-equality (PSEs) for both Separated and Combined conditions for all 20 subjects. Error bars are standard errors estimated from bootstrap analysis.

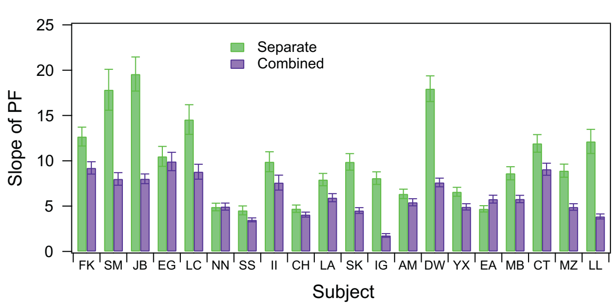

Fig. 5. Slopes of psychometric functions for Separated and Combined conditions for all 20 subjects. Error bars are standard errors derived from bootstrap analysis.

4.1. Explanation of the PSE difference

Before considering possible explanations for the PSE difference, note that in the Combined lattice at (or close to) the PSE (Fig. 1c), one observes not the red, cyan, violet and chartreuse colours associated with the poles of the S and L-M axes, but new colours: orange, green, magenta and blue. In the Combined lattices of the previous studies using a similar methodology (Kingdom et al., 2010; Schofield & Kingdom, 2012) the two components (colour and luminance; colour and texture; luminance and texture) were perceptually distinct at the PSE. In this study the presence of new colours in the Combined lattice patterns at the PSE raises the possibility that the difference in PSEs between the Separated and Combined conditions is caused by interactions among colour mechanisms intermediate in direction to those that encode the cardinal colours. The existence of intermediate, or 'higher-order' colour mechanisms is evidenced by both psychophysics (D'Zmura & Knoblauch, 1998; Gegenfurtner & Kiper, 1992; Goda & Fujii, 2001; Hansen & Gegenfurtner, 2006, 2012; Krauskopf & Gegenfurtner, 1992; Krauskopf et al., 1986; Lindsey & Brown, 2004; Webster & Mollon, 1991; see Eskew, 2009 for a critical review), and physiology (summarized by Gegenfurtner, 2003), the latter in the form of neurons as early as V1, though mainly in higher visual areas, that are tuned to a large variety of colour directions with narrow colour bandwidths.

The first possible explanation for the PSE difference that needs to be be considered is spatial resolution. In their Combined lattice stimuli Regan and Mollon (1997) found that the PSE shifted more towards the L-M component as the centre-to-centre circle separation was reduced, and conjectured that this was due to the poorer spatial resolution of the S system. The method employed here however controls for differences in L-M and S spatial resolution, precisely by comparing Separated and Combined conditions: any differences in L-M and S spatial resolution will apply equally to both conditions and will therefore be factored out.

The second possibility is that there is an interaction between the S and L-M sub-systems prior to the stage at which they are combined to signal the presence of intermediate colours. If this is the explanation, the interaction could occur in one of four ways: (a) a small suppression effect of L-M on S; (b) a small facilitation effect of S on L-M, (c) both S and L-M contrasts suppressed but the former slightly more than the latter, or (d) both S and L-M contrast facilitated but the latter slightly more than the former.

The third possibility to consider is that the PSE difference is due to interactions among higher-order colour mechanisms. Consider first mechanisms defined by intermediate axes within the DKL colour space. In our Combined lattice stimuli at the PSE these are close to the blue-orange and green-magenta axes shown in Fig. 1. Psychophysical evidence from hue scaling and discrimination studies has shown that we are relatively insensitive to variations along a bluish-yellowish axis (summarized in McDermott & Webster, 2012a), an axis close to that defined by the blue and orange circles in our stimuli. As can be seen in Fig. 2c however, the blue and orange circles form lines that lie along the horizontal and vertical, as do also the green and magenta circles. It is hard to see how a difference in sensitivity between the blue-orange and green-magenta axes could cause the PSEs to shift when going from the Separated to the Combined condition.

On the other hand, suppose the higher-order interactions were between adjacent poles of these intermediate axes. Studies have shown that colours group in inverse proportion to their perceptual distance (Stalmeier & de Weert, 1988; see also Bimler, Kirkland, & Pichler, 2004), so if the perceptual distance between orange and magenta, and/or between blue and green was smaller than between the alternative pairings, these pairs would tend to group together. Since these pairings form into obliquely-oriented lines in the Combined lattice (left-oblique in Fig. 2c) this would cause the PSEs to be biased in favour of the L-M component orientation (Fig. 2a). Webster (personal communication) has suggested that perhaps the 'warm' colours orange and magenta, and the 'cool' colours blue and green, separately group. Whatever the basis for grouping, the implication of this explanation is that the judgements in the Separated and Combined condition are of a fundamentally different nature, the former being concerned with the relative saliencies of L-M and S, the latter with the relative grouping strengths of different higher-order colour combinations.

In summary, the likely explanations for the difference in PSEs between Separated and Combined conditions are (1) an interaction between L-M and S prior to their combination into higher-order colour mechanisms; (2) grouping between blue and green, and/or between orange and magenta. Future experiments will be needed to test between these possibilities.

4.2. Relationship to previous studies

The previous studies most directly related to our Separated condition are the Switkes and Crognale (1999) study and a sub-set of the conditions in McDermott and Webster (2012b). With regard to our Combined condition, Regan and Mollon's (1997) study is the one most directly related. Using 1 cpd sinusoidal gratings Switkes and Crognale found that subjects matched L-M gratings with S gratings that were approximately 8 times higher in contrast, when contrast was defined as the vector sum $(L_c^2 + M_c^2 + S_c^2)^{1/2}$. If we convert our results into the vector sum metric, the corresponding average matching ratio for the Separated condition is 7.42, which is remarkably close to Switkes and Crognale. McDermott and Webster (2012b) required subjects to match the saliencies of chromatic $1/f$, or 'pink' noise patterns with that of a common standard in the form of a $1/f$ luminance pattern. Their Fig. 4 suggests that the S and L-M contrasts were more-or-less equally salient when measured this way. Their contrasts however were defined according to the original MacLeod-Boynton colour space, whose axes are $S/(L+M)$ or $L/(L+M)$. The S cone excitation in the MacLeod-Boynton colour space is scaled very differently to that here, so it is difficult to make a direct comparison with the results of McDermott and Webster (2012b). A similar difficulty arises in comparing our Combined condition with the results of Regan and Mollon (1997). It is important to emphasize however that when making comparisons with previous studies it is the *comparison* of the Separated and Combined conditions that is the hallmark of the present study. For this purpose it does not matter how the axes are scaled, but more importantly, studies that are comparable to *either* the Separated or Combined *but not both* conditions have little direct bearing upon the present results. Finally, an anonymous reviewer remarked that the ranges of log[S/(L-M)] employed here as well as the resulting PSEs are similar to the ranges and PSEs for the S versus luminance condition in Kingdom et al. (2010), where luminance was defined as $L_c + M_c + S_c$. This reflects the fact that the balance-point between LUM and L-M in Kingdom et al. (2010) was close to unity (zero in log units).

This study deals with appearance. Are there related performance studies? Chen, Foley, and Brainard (2000a, 2000b) measured detection thresholds for Gabor patterns defined by S or L-M contrasts in the presence of masks of the same or opposite cardinal direction. They found strong suppressive masking of L-M targets by high contrast S masks, but due to limitations in the range of their monitor they were unable to explore the converse situation for high contrast L-M masks with S targets. Therefore it is difficult to compare the results of Chen et al. with those of the present study.

4.3. Limitations of study

What are the limitations of this study? Our results were obtained using a particular stimulus configuration in which the dominant orientations of the two colour components were orthogonal. We cannot be certain therefore that the same results would be

Table 1
Ranges of L-M and S contrasts employed for each subject. The last column shows the range in terms of the logarithm of the ratio of S to L-M contrasts, computed as the range between $\log 10[S_{min}/(L\text{-}M)_{max}]$ and $\log 10[S_{max}/(L\text{-}M)_{min}]$.

Subject	L-M range	S range	Log S/(L-M) range
FK	0.05–0.15	0.25–0.75	0.222–1.176
SM	0.05–0.15	0.25–0.75	0.222–1.176
JB	0.05–0.15	0.25–0.75	0.222–1.176
EG	0.05–0.15	0.25–0.75	0.222–1.176
LC	0.05–0.15	0.25–0.75	0.222–1.176
NN	0.0117–0.175	0.05–0.75	−0.544 to 1.807
SS	0.0117–0.175	0.05–0.75	−0.544 to 1.807
II	0.0117–0.175	0.05–0.75	−0.544 to 1.807
CH	0.0117–0.175	0.05–0.75	−0.544 to 1.807
LA	0.03–0.15	0.15–0.75	0.0–1.398
SK	0.03–0.15	0.15–0.75	0.0–1.398
IG	0.03–0.15	0.15–0.75	0.0–1.398
AM	0.0117–0.175	0.05–0.75	−0.544 to 1.807
DW	0.045–0.1	0.225–0.5	0.0–1.398
YX	0.03–0.15	0.15–0.75	0.0–1.398
EA	0.03–0.15	0.15–0.75	0.0–1.398
MB	0.03–0.15	0.15–0.75	0.0–1.398
CT	0.045–0.1	0.225–0.5	0.352–1.046
MZ	0.03–0.15	0.15–0.75	0.0–1.398
LL	0.03–0.15	0.15–0.75	0.0–1.398

obtained if the components were spatially aligned, although it seems reasonable to suppose that they would, since the elements of the patterns were circular patches with combined L-M and S colours. The stimulus/task we have employed in this study does not lend itself easily to testing for interactions between spatially-aligned suprathreshold colours, so the effects of spatial alignment must await a different experimental approach. Another arguable limitation of the present study is that we have not explored the interaction between L-M and S colours across the full range of colour contrast levels. It is possible that the nature of the interaction we have revealed is not independent of contrast level. This possibility must await further investigation.

Acknowledgments

The research was supported by Canadian Institute of Health Research Grants MOP 82755 and MOP 123349 awarded to FK. Special thanks to Mike Webster and two anonymous referees for their many useful comments and suggestions on earlier drafts of the manuscript.

Appendix A

See Table 1.

References

Bimler, D., Kirkland, J., & Pichler, S. (2004). Escher in color space: Individual-differences multidimensional scaling of color dissimilarities collected with a Gestalt-formation task. *Behavioral Research Methods, Instruments & Computers, 36*, 69–76.

Chen, C.-C., Foley, J. M., & Brainard, D. H. (2000a). Detection of chromoluminance patterns on chromoluminance pedestals I: Threshold measurements. *Vision Research, 40*, 773–788.

Chen, C.-C., Foley, J. M., & Brainard, D. H. (2000b). Detection of chromoluminance patterns on chromoluminance pedestals II: Model. *Vision Research, 40*, 789–803.

Cole, G. R., Hine, T., & McIlhagga, W. (1993). Detection mechanisms in L-, M-, and S-cone contrast space. *Journal of the Optical Society of America A, 10*, 38–51.

Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology, 357*, 241–265.

D'Zmura, M., & Knoblauch, K. (1998). Spectral bandwidths for the detection of color. *Vision Research, 38*, 3117–3128.

Eskew, R. T. Jr., (2009). Higher order color mechanisms: A critical review. *Vision Research, 49*, 2686–2704.

Eskew, R. T., McLellan, J. S., & Giulianini, F. (1999). Chromatic detection and discrimination. In K. Gegenfurtner & L. T. Sharpe (Eds.), *Color vision: From molecular genetics to perception* (pp. 345–368). Cambridge: Cambridge University Press.

Gegenfurtner, K. R. (2003). Cortical mechanisms of colour vision. *Nature Reviews Neuroscience, 4*, 563–572.

Gegenfurtner, K. R., & Kiper, D. C. (1992). Contrast detection in luminance and chromatic noise. *Journal of the Optical Society of America A, 9*(11), 1880–1888.

Goda, N., & Fujii, M. (2001). Sensitivity to modulation of color distribution in multicolored textures. *Vision Research, 41*, 2475–2485.

Gorea, A., & Papathomas, T. V. (1991). Extending a class of motion stimuli to study multiattribute texture perception. *Behavioral Research Methods, Instruments, & Computers, 23*, 5–8.

Hansen, T., & Gegenfurtner, K. R. (2006). Higher level chromatic mechanisms for image segmentation. *Journal of Vision, 6*(3), 239–259 (article no. 5).

Hansen, T., & Gegenfurtner, K. R. (2012). Higher-order color mechanisms: Evidence from noise masking experiments in cone contrast space. *Journal of Vision, 13*(1) (article no. 26).

Kingdom, F. A. A., Bell, J., Gheorghiu, E., & Malkoc, G. (2010). Chromatic variations suppress suprathreshold brightness variations. *Journal of Vision, 10*(10), 1–13 (article no. 13).

Kingdom, F. A. A., Rangwala, S., & Hammamji, K. (2005). Chromatic properties of the colour shading Effect. *Vision Research, 45*, 1425–1437.

Krauskopf, J., & Gegenfurtner, K. (1992). Color discrimination and adaptation. *Vision Research, 32*, 2165–2175.

Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of colour space. *Vision Research, 22*, 1123–1131.

Krauskopf, J., Williams, D. R., Mandler, M. B., & Brown, A. M. (1986). Higher order color mechanisms. *Vision Research, 26*, 23–32.

Lindsey, D. T., & Brown, A. M. (2004). Masking of grating detection in the isoluminant plane of DKL color space. *Visual Neuroscience, 21*, 269–273.

MacLeod, D. I. A., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 60*, 1183–1186.

McDermott, K. C., & Webster, M. A. (2012a). Uniform spaces and natural image statistics. *Journal of the Optical Society of America A, 29*, 182–187.

McDermott, K. C., & Webster, M. A. (2012b). The perceptual balance of color. *Journal of the Optical Society of America A, 29*, A108–117.

Mollon, J. D. (1995). Seeing color. In T. Lamb & J. Bourriau (Eds.), *Colour, art and science* (pp. 127–150). London: Cambridge Univ. Press.

Mullen, K. T., & Sankeralli, M. J. (1999). Evidence for the stochastic independence of the blue–yellow, red–green and luminance detection mechanisms revealed by subthreshold summation. *Vision Research, 39*, 733–745.

Norlander, C., & Koenderink, J. J. (1983). Spatial and temporal discrimination ellipsoids in color space. *Journal of the Optical Society of America, 73*, 1533–1543.

Papathomas, T. V., & Gorea, A. (1988). Simultaneous motion perception along multiple attributes: A new class of stimuli. *Behavioral Research Methods, Instruments, & Computers, 20*, 528–536.

Papathomas, T. V., Kovács, I., Gorea, A., & Julesz, B. (1995). A unified approach to the perception of motion, stereo, and static-flow patterns. *Behavior Research Methods, Instruments & Computers, 27*, 419–432.

Prins, N. & Kingdom, F. A. A. (2009). *Palamedes: Matlab routines for analyzing psychophysical data*. <http://www.palamedestoolbox.org/>.

Regan, B. C., & Mollon, J. D. (1997). The relative salience of the cardinal axes of colour space in normal and anomalous trichromats. In C. R. Cavonius (Ed.), *Colour vision deficiencies XIII* (pp. 261–270). Dordrecht: Kluwer Academic Publishers.

Sankeralli, M. J., & Mullen, K. T. (1997). Postreceptoral chromatic detection mechanisms revealed by noise masking in three-dimensional cone contrast space. *Journal of the Optical Society of America A, 14*, 906–915.

Schofield, A. J., & Kingdom, F. A. A. (2012). Texture dominates saliency in suprathreshold combinations of texture, color and luminance. *Journal of Vision, 12*(9) (article no. 1290).

Smith, V. C., & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 700 nm. *Vision Research, 15*, 161–171.

Stalmeier, P. F. M., & de Weert, C. M. M. (1988). Large colour differences measured by spontaneous Gestalt formation. *Color Research & Application, 13*, 209–218.

Stromeyer, C. F., III, Cole, G. R., & Kronauer, R. E. (1985). Second-site adaptation in the red–green chromatic pathways. *Vision Research, 25*, 219–237.

Switkes, E. (2008). Contrast salience across three-dimensional chromoluminance space. *Vision Research, 48*, 1812–1819.

Switkes, E., & Crognale, M. A. (1999). Comparison of color and luminance contrast: Apples versus oranges? *Vision Research, 39*, 1823–1831.

Webster, M. A., & Mollon, J. D. (1991). Changes in colour appearance following post-receptoral adaptation. *Nature, 349*, 235–238.