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Foveal spatial summation in human cone mechanism

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Abstract. We measured at the fovea the chromatic contrast threshold for stimuli modulated along different chromatic directions in the isoluminant plane of MBDKL colour space, considering the two cardinal axes (L/M) and $S/(L+M)$ and other intermediate non-cardinal directions. This psychophysical determination was conducted as a function of stimulus size. The test stimulus was a foveal isoluminant Gaussian patch with a raised cosinusoidal temporal profile superimposed on a neutral background. The task was performed binocularly. The increment threshold was measured for three observers by a Bayesian adaptive psychometric method (QUEST). The Ricco area of complete spatial summation was estimated from the threshold-versus-area curves. The perceptive fields are smaller for the L/M-cone opponent direction than the $S/(L+M)$-cone opponent. The perceptive field sizes for the stimuli in non-cardinal chromatic directions and stimuli modulated at the (L/M)-cone opponent direction present similar values. Measurements were made at two luminance levels, 5 and 40 cd m^{-2}, but the differences found were small. The perceptive field sizes found could be associated with LGN area.

1 Introduction

The threshold for detecting the chromatic difference between neutral background and isoluminant coloured stimuli, as a function of stimulus size, is a good method for perceptive field estimation. The perceptive field values that result from psychophysical measures are known as the subjective correlates of receptive fields. They are also defined as the complete summation area. The perceptive fields related to the colour mechanisms are larger than the receptive fields from anatomical estimation (Abramov et al 1991).

The concept of complete summation area is used to show that the psychophysical result from the determination of the threshold for small-test lights depends on a constant amount of light energy which is independent of its spatial distribution over a finite sector of the retina. Two psychophysical laws are usually considered as related to spatial summation when the threshold is measured by light increments or decrements (Brindley 1954; Vassilev et al 2000, 2003, 2005; Volbrecht et al 2000, 2009). According to Ricco's law, or law of compensation, the threshold luminance of a stimulus is inversely proportional to its area, so that its spatial distribution does not have any influence on the threshold luminous flux. Ricco's area or complete summation area is the largest area up to which this law holds. Outside Ricco's area of spatial summation the results follow approximately Piper's law. This states that the threshold luminance of the stimulus is inversely proportional to the square root of its area (Vassilev et al 2000).

The size of Ricco's area (Ricco 1877) has usually been interpreted according to the degree of overlap between the receptive fields of ganglion cells or some other retinal neurons or as a convergence of signals of the visual field from nearby points onto a common pathway (Schefrin et al 1998).

Volbrecht et al (2000), using Stiles two-colour threshold method to isolate the activity of the S-cone (Stiles 1949), psychophysically measured the complete summation area for short-wavelength-sensitive (S) and long-wavelength-sensitive (L) cone mechanisms at the fovea and up to 20 deg along the vertical meridian in the superior retina. The results, using the incremental threshold as a function of the stimulus's area, show that Ricco's area is bigger for the S-cone mechanism than for the L-cone mechanism for all retinal eccentricities. These results reflect a difference in ganglion cell density and changes in neuronal convergence at all retinal locations. The size of the perceptive field obtained at the central fovea was approximately 0.46 deg for stimuli that activate the S-cone and, in the case of activated L-cone, the perceptive field is smaller, about 0.1 deg.

Vassilev et al (2003), also using the Stiles two-colour threshold method, conducted an experiment at different eccentricities (from 0 deg to 20 deg). These results showed that the spatial summation of S-cone increment, within the 0 – 5 deg range, was approximately the same value ($\sim$0.37 deg) as for S-cone decrement which is about 0.32 deg. However, this difference increased beyond this range. The S-cone on – off asymmetry in spatial summation was only found at the retinal periphery (Vassilev et al 2003).

Vassilev et al (2000) and Volbrecht et al (2000) show that the difference in the size of Ricco's area between the S-cone mechanism and the L-cone one cannot be attributed to the inherent chromatic aberration of the eye. An analysis of their data suggests that the sizes of Ricco's area for both cone mechanisms are more likely mediated by ganglion cell density. The summation area associated with the L-cone mechanism is directly related to the reciprocal of midget and parasol ganglion cell density.

While in all previous works the S-cones were isolated by the Stiles two-colour method, Vassilev et al (2005) used an isoluminant stimulus. The stimuli were presented against a neutral background at a range of eccentricities of 5 deg to 30 deg in the horizontal temporal retinal meridian. They measured the S-cone contrast threshold for stimuli of different sizes, modulated along the white – 90° direction in the isoluminant plane of MBDKL colour space. The cone contrast was defined as an incremental cone excitation divided by the cone excitation of the background. Ricco's areas are approximately 0.3 to 0.4 deg for S-cone at 5 deg of eccentricity, increasing up to 1.3 deg for 30 deg eccentricity. The authors found that, despite applying different methods to isolate stimulation of S-cones, an isoluminant stimulus or Stiles two-colour threshold method, the perceptive field values were independent of them and, as a consequence, yielded a similar estimation.

The perceptive fields have also been extensively analysed by means of visual appearance experiments for chromatic stimuli (Abramov et al 1989, 1991). These authors measured the appearance of spectral light presented to the fovea and at different eccentricities as a function of stimulus sizes using hue and saturation scaling. Abramov et al (1991) compared the perceptive field sizes to known sizes of receptive fields in the retina, LGN, V1, V4 and concluded that perceptive fields are not determined at retinal level, associating them with areas V1 and V4. These results are in agreement with the fact that the unique hues do not coincide with colour tuning by the sub-cortical chromatic mechanisms found in LGN neurons. The unique hues can be explained postulating higher-order colour mechanisms (Abramov and Gordon 2005; Wuerger et al 2005; Volbrecht et al 2009).

Although perceptive chromatic fields have been extensively studied, as we can see from the preceding results we could not find enough systematic studies of perceptive fields estimated from chromatic sensitivity as a function of the isoluminant stimulus size modulated in cardinal chromatic mechanisms [L/M and $S/(L+M)$], and non-cardinal directions. Like Vassilev et al (2005), in the present study we isolated the cone activation, presenting isoluminant stimuli modulated in colour along cardinal axes. We determined the thresholds for detecting a chromatic difference along a particular direction in colour space, that is the threshold for distinguishing between a neutral background and an isoluminant chromatic stimulus defined by a particular hue. The experiment was carried out with two adaptation luminances, 5 cd m^{-2} (high mesopic value) and 40 cd m^{-2} (photopic value).

This study differs from previous studies involving spatial summation in that it measures perceptive fields along several directions in MBDKL space. We measured perceptive field size along both cardinal and other non-cardinal axes, filling in the gap that existed in the previous works. The potentially interesting result relates to the perceptive field size for $0° - 180°$ axis stimuli, $190° - 270°$ axis stimuli, and the non-cardinal axes.

2 Experiment and data

2.1 *Stimuli*

The stimuli were presented on an achromatic background on a high-resolution colour monitor (EIZO T560i) controlled by a graphic video card (VSG 2/3, Cambridge Research Systems). The characteristics of the phosphors were measured with an LMT 1200 colour metre and the monitor was calibrated via gamma-corrected look-up tables. The phosphor CIE chromaticity coordinates were (0.64; 0.34), (0.30; 062), and (0.20; 0.09), for the red, green, and blue colour guns, with a maximum luminance of 47.8 cd m^{-2}, 142.7 cd m^{-2}, and 19.4 cd m^{-2}, respectively. The monitor had a high pixel resolution with a frame rate of 75 Hz and a line rate of 60 kHz. The coordinates for the background were (0.35; 0.37) perceived as white. We used the same stimulus as those used in previous studies (O'Donell and Colombo 2008; O'Donell et al 2010). The stimulus was a circular patch with a spatial Gaussian profile, including four sizes of the stimulus with $SD = 0.129$ deg; 0.258 deg; 0.522 deg; and 1.045 deg, with a maximum hue modulation at the centre. We blurred the stimulus to minimise luminance transients that might occur in the retinal image of the stimulus owing to transversal chromatic aberrations (Knoblauch et al 1991). In addition, the effects of temporal transients were minimised by presenting the stimulus with a raised cosinusoidal temporal profile, so that hue modulation reached a maximum at 300 ms after stimulus onset, thus facilitating the detection through chromatic channels (King-Smith and Carden 1976). The stimulus remained under this condition for a further 300 ms and was reduced over the final 300 ms of the presentation.

The stimuli were generated in the central region of the monitor, which is spatially homogeneous, over an achromatic neutral background of 5 and 40 cd m^{-2}. The monitor subtended 7.7 deg in width and 10.3 deg in height at 200 cm from the observer for the two smallest stimuli and, for the two larger stimuli, it was placed at a visual distance of 100 cm from the subject, subtending an adapting field of 15.4 deg × 20.4 deg. The dimensions of the monitor were 360 mm in height and 270 mm in width. The chromatic coordinates (x, y) of the stimuli were specified in the isoluminant CIE 1931 colour space, as shown in figure 1. The chromatic coordinates of the stimuli used to measure chromatic detection are found on the line that joins white (W) with each of the points. Stimuli lying along 0° and 180° axes (Derrington et al 1984) are located on the axis that produces excitation of the L- and M-cone ($L - M$-cone opponent mechanism). The axis corresponding to the $[S - (L + M)]$-cone opponent mechanism belongs to the conventional tritanopic line. The stimuli lying along 90° and 270° axes are located on this tritanopic line. The remaining stimuli are found in intermediate positions. The stimuli modulated in the cardinal axes have a reddish (0°), greenish blue (180°), violet (90°), and lime (270°) appearance.

The chromatic threshold detection measured is quantified in terms of the length of a stimulus vector called pooled contrast:

$$\mathrm{RMS} = \left\{\tfrac{1}{3}\left[(\Delta L/L_0)^2 + (\Delta M/M_0)^2 + (\Delta S/S_0)^2\right]\right\}^{1/2}, \qquad (1)$$

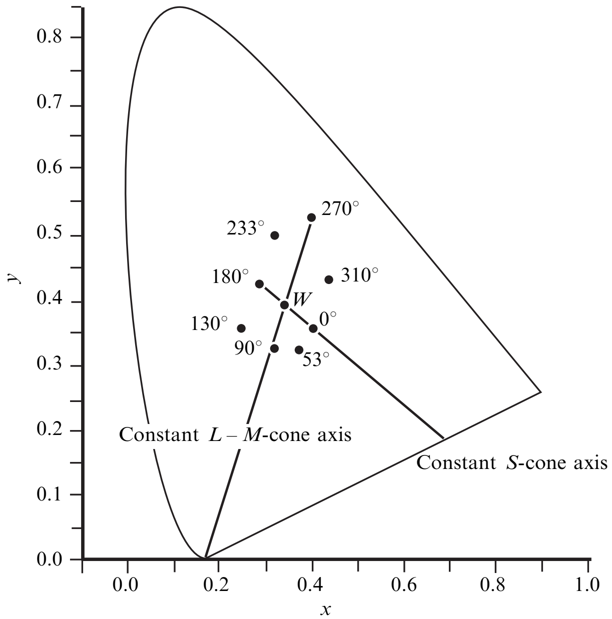

Figure 1. Chromatic coordinates of the stimuli in the CIE 1931 colour spaces used to measure chromatic detection.

where $\Delta L/L_0$, $\Delta M/M_0$, $\Delta S/S_0$ are the Weber cone contrasts produced by each stimulus on the background. Cone contrast has been widely adopted as a metric for the specification of chromatic stimuli. These data were computed as Weber cone contrasts produced by each stimulus on the neutral background. Cone excitations were calculated using the Judd-modified 1931 CIE values in conjunction with the Smith and Pokorny (1972) fundamentals. To produce a single value for the specification of cone contrast for each stimulus, we computed the pooled root-mean-square (RMS). This quantity is the square-root of the cone contrast energy and is closely related to the vector-length model of colour thresholds (Poirson et al 1990).

Since RMS cone-contrast depends on chromatic direction and luminance contrast, we chose the isoluminant RMS cone contrast (RMS_i) to represent the threshold chromatic contrast in each direction with no change of luminance between stimulus and background. This isoluminant condition was determined by heterochromatic flicker photometry that will be explained in section 2.3. This is the luminance value of the chromatic stimulus that each observer matches to the background luminance on which the stimulus was presented.

2.2 *Subjects*

Three subjects participated in the experiments (BO: female, 50 years old; MC: male, 25 years old; and BT: male, 25 years old). The subjects were one of the authors and two observers unaware of the purpose of the experiment.

All the observers tested colour normal on the FM-100 hue tests, and all were well trained in the task before the collection of the data reported here. We also used a straylight meter (Oculus C-Quant) to measure the amount of straylight for observer BO. The result showed that this observer had normal values for her age. The stimuli were viewed foveally and binocularly with natural pupils. The protocol was in accordance with the provisions of the World Medical Association Declaration of Helsinki of October 2008.

2.3 *Psychophysical procedure*

The chromatic detection threshold was measured by the Bayesian adaptive method (QUEST—Watson and Pelli 1983). This method combines the experimenter's prior knowledge of the appropriate stimulus range and the observer's response, in past trials, in choosing the signal strength for the next trial. In this method, the threshold is treated as a normally distributed random variable. After each response, the threshold's Gaussian probability density function is updated using Bayes's rule to integrate the prior (or probability of detection) information.

The test stimulus was superimposed on the 'white' adapting field. The room was kept dark so that the adaptation luminance was provided by the area subtending the entire monitor screen. The observer's task was a typical detection task with "yes – no" responses. The adaptation background, 5 or 40 cd m^{-2}, was always present to assure the adaptation to a given value.

This method requires the knowledge of an approximate first threshold value. In order to estimate this value, it is necessary to carry out pilot experiments before starting each experimental sequence.

For each chromatic direction, size of the stimulus, and adaptation luminance the number of stimuli presented was fixed at 20 (Watson and Pelli 1983), with values near to the one that resulted from the pilot experiment. Thus, each stimulus had the same chromatic direction, size, and adaptation luminance, differing only in purity excitation. Each of these 20 stimuli was modulated for each chromatic direction (the line that joins the white reference and the colour involved) with purity excitation varying from 4% to 0.1%, close to the value previously determined in a pilot experiment.

It is necessary to determine first the isoluminant condition for all of them. For each observer, the luminance of these fixed 20 stimuli was matched to the background by heterochromatic flicker photometry. The stimulus presented was pulsed on and off at 15 Hz and the luminance of the stimulus was adjusted until the perceptual flicker was minimised. The standard deviation of these isoluminance experimental values was around 1%.

Each experimental session began with a choice at random of the stimulus colour and the adaptation luminance. The observer first made the heterochromatic flicker photometry experiment with all the stimuli, in order to obtain the isoluminant condition for each one. The observers were adapted for 5 min to the adapting field, prior to the beginning of the data collection, and were instructed to fixate on the centre of the display. Their head position was maintained with a chin-rest. The entire monitor was illuminated and was not occluded from the observers' view.

The threshold measurement for each size of the stimulus was repeated five times. Each experimental session took approximately 15 min for each colour, stimulus size, and adaptation luminance.

In order to avoid chromatic aftereffects we chose an inter-trial time of 800 ms after the observers' response since, according to Fairchild and Reniff (1995) the chromatic adaptation at constant luminance was 90% complete after approximately 60 s. In this way, we can guarantee that chromatic adaptation does not occur.

The threshold values measured are given, first in terms of the chromatic coordinates (x, y) in the CIE 1931 colour space. $\mathrm{RMS_i}$ cone contrast was calculated using Judd-transformed x, y values of the ends of the vector and deriving long-, medium-, and short-wavelength cone excitations based on Smith – Pokorny fundamentals (Smith and Pokorny 1972). Weber contrast was derived for the three cone classes and the $\mathrm{RMS_i}$ calculated using equation (1).

3 Results

The results are shown in figure 2, as log detection threshold versus log stimulus area for each observer, chromatic direction, and adaptation luminance. Each point corresponds to a mean value. We fitted each set of experimental data presented in figure 2 with an exponential function as a function of log area (x):

$$\log \mathrm{RMS_i} = \log \mathrm{RMS_{i_0}} + A \exp(-x/t) \,, \tag{2}$$

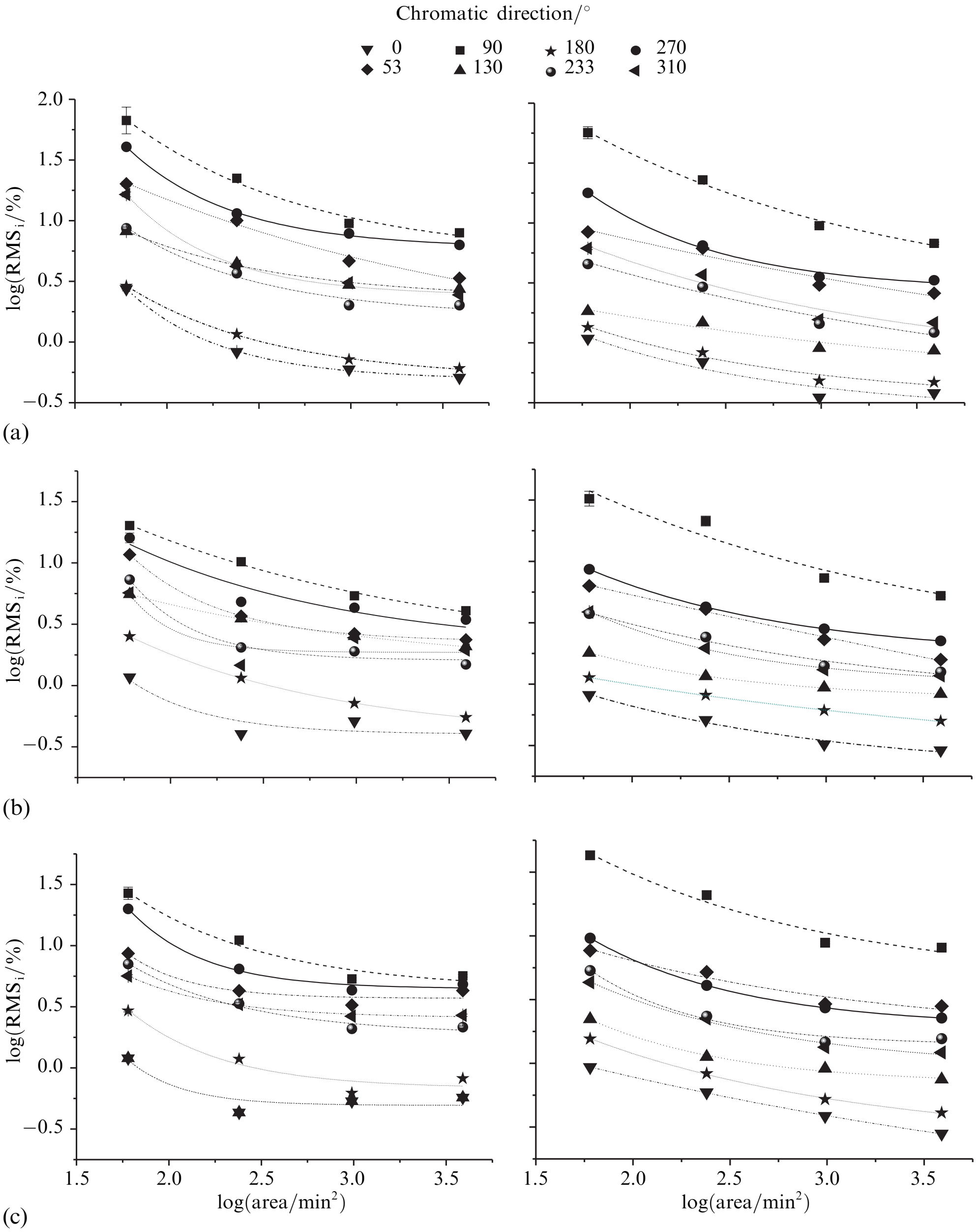

Figure 2. Log detection threshold versus log stimulus area for each observer. The error bars represent ±1 SEM for observers BO (a), BT (b), and MC (c), at different luminances: 5 cd m^{-2} (left) and 40 cd m^{-2} (right).

where $\log \mathrm{RMS}_{\mathrm{i}_0}$ is the asymptotic value of $\log \mathrm{RMS}_{\mathrm{i}}$, t is related to the growth speed, and A is a scale factor. The fitted curve is purely a mathematical description of the psychophysical behaviour, with no link to the underlying physiological substrates.

In all cases, the threshold to detect the chromatic stimulus is smaller at 40 cd m^{-2} than at 5 cd m^{-2} and also for stimuli modulated on the L/M-cone opponent axis, than for those modulated on the S-cone opponent axis. Non-cardinal stimuli have threshold values between the two cardinal axes.

The chromatic threshold data found were subjected to an analysis of covariance (ANCOVA) in a general linear model, with $\log(\mathrm{RMS_i}/\%)$ as a dependent variable, log (area) as a continuous predictor variable (covariate), and chromatic direction, size, and adaptation luminance as categorical independent variables (factors). This statistical analysis shows a significant effect of the covariate [log (area)], on the dependent variable $\log(\mathrm{RMS_i}/\%)$ ($F_{1,578} = 1595$, $p < 0.05$), with chromatic direction ($F_{7,578} = 824.95$, $p < 0.05$), adaptation luminance ($F_{1,578} = 209.65$, $p < 0.05$), and observer ($F_{2,578} = 104.94$, $p < 0.05$). The major differences are due to the chromatic directions, while the changes due to either the observers (33% between observers BO and BT; 3% between observers BT and MC) or the adaptation luminance (2% between both adaptation luminances) are smaller.

3.1 *Perceptive fields*

The perceptive fields were estimated as follows: since we have only four points for each experimental condition and observer, and since equation (1) fits the experimental data quite well, we have simulated data of $\log(\mathrm{RMS_i}/\%)$ as a function of $\log(\mathrm{area/min^2})$. The perceptive field procedure is depicted in figure 3. We have provided this run as an example because it contains some modest outliers. Figure 3 shows only two chromatic situations as representative of the method used to calculate perceptive fields (90° and 0°, both adaptation luminance and observer BO). Figure 3 also includes experimental data from figure 2.

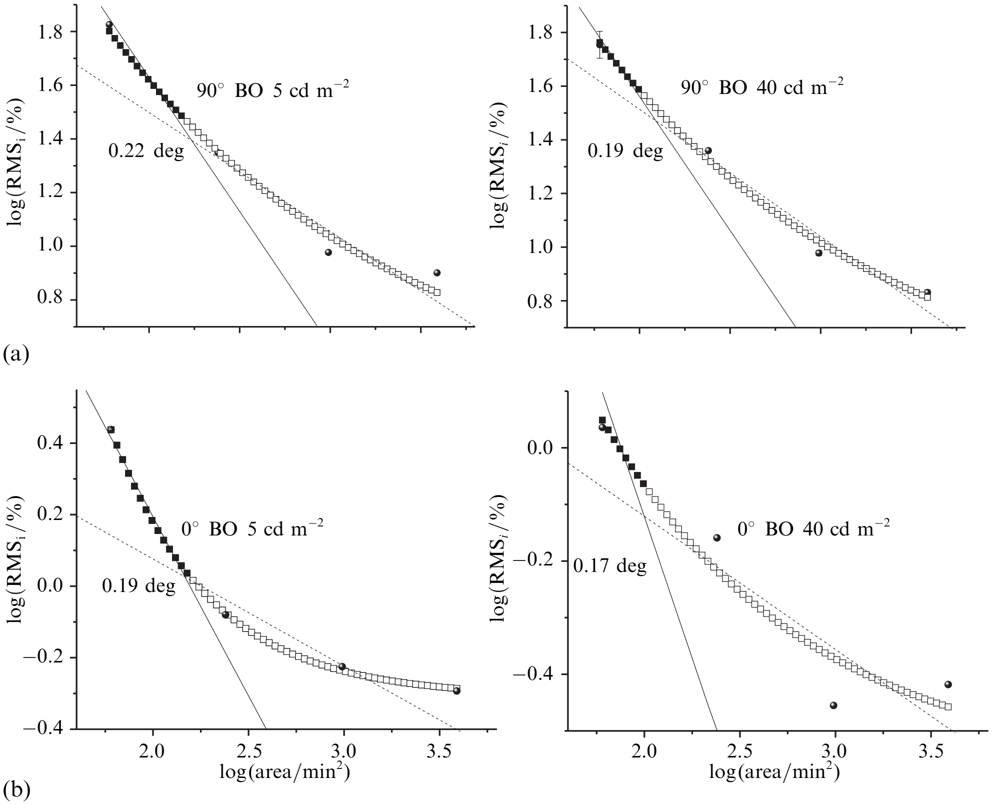

Figure 3. $\log(\mathrm{RMS_i}/\%)$ as a function of $\log(\mathrm{area/min^2})$ for chromatic axis: (a) 90 deg, (b) 0 deg, considering both adaptation luminance and the observer BO. Experimental data from figure 2 are shown as circles.

Ricco's law of spatial summation states that, for sufficiently small stimulus sizes, the threshold is inversely related to the stimulus area; that is, the threshold luminous flux is constant (Ricco 1877). For stimuli larger than Ricco's area, the relevant noise is proportional to the stimulus area and the threshold is inversely proportional to the area to the power of 0.5; that is, it obeys Piper's law (Barlow 1957, 1958; Glezer 1965). The two lines, through each set of the simulated data points shown in figure 3, are the least-squares fit determined by the two-phase linear regression model (Seber and Wild 1989) and represent both laws, the first being Ricco's law and the second Piper's law.

The slope of the first line was fixed at -1. The slope of the second line and the point of intersection of the two lines were allowed to vary. The points along the second line closely followed Piper's law; nevertheless, all the values of this slope are lower than expected from Piper's law and equal to 0.26 with SD = 0.02. The intersection of the two lines was assumed to provide an estimate of the area of complete summation, that is Ricco's area. The bilinear approximation fits the simulated data well (mean $R^2 = 0.98$; SD = 0.02). These second slope values were subjected to an analysis of variance (ANOVA) in a general linear model with chromatic direction, size, and adaptation luminance as categorical independent variables (factors). In this way, these second slopes do not present significant differences for the observer, for chromatic directions, or for adaptation luminance.

Following the procedure explained in figure 3, we have estimated the perceptive fields of all stimuli and conditions (table 1).

Table 1. Perception fields for all stimuli and conditions.

Adaptation luminance/cd m^{-2}	Chromatic direction/°	Perceptive field/min		
		BO	BT	MC
5	0	11.2	11.7	10.7
	53	11.1	11.2	11.2
	90	13.0	12.3	12.7
	130	10.8	10.0	10.0
	180	9.4	11.0	11.2
	233	11.2	11.2	11.6
	270	13.0	12.3	13.3
	310	13.0	11.5	10.8
40	0	10.0	9.5	8.5
	53	8.5	9.0	9.2
	90	11.2	11.2	11.5
	130	8.4	8.1	9.3
	180	9.3	8.4	9.3
	233	8.8	8.6	11.3
	270	12.6	10.6	11.7
	310	9.3	9.7	10.0

Table 1 shows the perceptive field for each observer. These values were subjected to a three-way ANOVA. The ANOVA indicated significant main effects of adaptation luminance ($F_{1,37} = 83.61$, $p < 0.05$) and chromatic direction ($F_{7,37} = 14.24$, $p < 0.05$) but did not show a significant difference between observers. There is no interaction between the chromatic direction and the adaptation luminance, which is consistent with the hypothesis that colour and luminance are processed independently.

Mean perceptive field sizes for each chromatic axis, taking the adaptation luminance as parameters, are plotted in figure 4. Each value is the average for all observers.

This figure shows that the perceptive field size necessary to detect a chromatic stimulus is larger for 90° and 270° than for 0° and 180° stimuli. The perceptive fields that correspond to the non-cardinal stimuli present values closer to the stimuli along 0° – 180° axes. This result implies that the summation area along the non-cardinal directions seems to be aligned with the summation area for L/M direction.

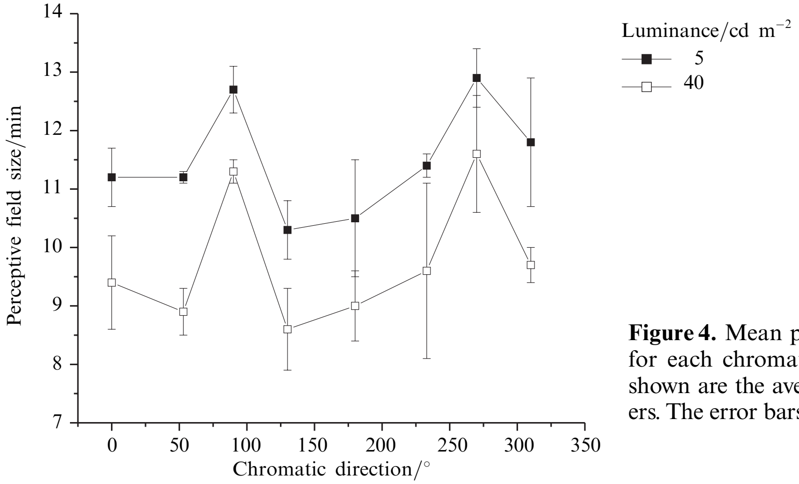

Figure 4. Mean perceptive field sizes for each chromatic axis. The values shown are the averages for all observers. The error bars represent ±1 SEM.

Table 2 shows the Tukey post-hoc analysis (or multiple comparison test) within the different chromatic directions. We can see that there is statistically no difference between 0° and 180° and between 90° and 270°, while the intermediate chromatic stimuli display significant differences solely with the stimuli corresponding to the line 90° – 270°.

Table 2. A posteriori Tukey test within chromatic directions.

Chromatic direction/°	Chromatic direction							
	0	53	90	130	180	233	270	310
0								
53	0.998607							
90	**0.005012**	**0.001044**						
130	0.443586	0.810438	**0.000147**					
180	0.909356	0.997837	**0.000267**	0.989579				
230	0.999818	0.962699	**0.015879**	0.218693	0.689363			
270	**0.000872**	**0.000256**	0.997122	**0.000139**	**0.000153**	**0.002714**		
310	0.959792	0.706333	0.070052	0.061205	0.316275	0.998362	**0.013731**	

4 Discussion

We found that the perceptive fields estimated from chromatic threshold/stimulus size measurements are divided into two groups associated with the two chromatic mechanisms: the S-cone mechanism and the L/M-cone mechanism. The spatial summation area upon selective stimulation of the S-cone mechanism takes place over larger areas than the spatial summation for the L/M-cone mechanism, in agreement with Volbrecht et al (2000), who showed that the spatial summation is greater when the S-cone mechanism is stimulated selectively than when the L-cone mechanism is stimulated.

The blue/yellow bistratified ganglion cells receive excitatory input from the S cones and represent approximately 1% to 3% of the ganglion cells in the central retina, while M and L cones send their input to the midget ganglion cells and the parasol ganglion cells.

The midget ganglion cells account for 90% of the human ganglion cells in the central retina, whereas the parasol ganglion cells account for only 5% to 6% of the human ganglion cells in the central retina. As mentioned by Volbrecht et al (2000) and Fischer (1973), the difference between the two groups of summation areas found in the present study may be related to ganglion cell density, which provides the neural weights for these colour mechanisms. The blue/yellow perceptive fields form one group and the green/red ones form another. In this study, it would be possible to associate the values of perceptive fields at the LGN process level. The variations of summation area along the whole range of chromatic directions occur in two well-differentiated groups. The segregation of these two groups could be reflecting these separate pathways, thus supporting the hypothesis that colour processing reflects the cone-opponent processing. If the summation area occurred at a higher level of colour processing, the summation area of the non-cardinals axes would be different from the L/M channel. This post-opponent reorganisation is viewed in terms of the generation of multiple 'higher order' chromatic mechanisms, tuned to a wide variety of axes in colour space. We will return to this issue later on.

The perceptive fields estimated from non-cardinal stimuli are found in the group corresponding to the L/M chromatic channel. This means that, at the fovea, the perceptive field values along non-cardinal directions seem to be aligned with the L/M chromatic channel. When stimuli are modulated along the $[S-(L+M)]$ opponent axis, more information would be necessary to detect them than in the case of the stimuli modulated on the $(L-M)$ opponent axis. This would be probably a consequence of the difference of density or/and the cone distribution on the retina. Mullen and Kingdom (2002) suggest that the distribution of the $(L-M)$- and $[S-(L+M)]$-cone opponency across the visual field is very different. While the $(L-M)$-cone opponent mechanism can be considered as a foveal specialisation, $[S-(L+M)]$-cone opponency is more uniformly distributed across the visual field, and more closely resembles the distribution of the achromatic system. Anatomical studies of the human retina have revealed that L- and M-cones reach their maximum density in the central part of the fovea, whereas S-cone density has a peak at approximately 1 deg of eccentricity and is zero at the tritanopia zone (0.35 deg) (Curcio and Allen 1990). These inhomogeneities may produce differences between the summation areas obtained with $(L-M)$- and $[S-(L+M)]$-cone opponents. If the summation areas for the non-cardinal directions are similar to those in the L/M direction, we can speculate that this assertion seems to imply that the convergence of receptors from $L-M$ cones has a greater influence than that from S-cones.

The greater perceptive fields correspond to the stimuli lying along $90^\circ-270^\circ$ axes, equal to 0.21 deg, while the values for $0^\circ-180^\circ$ axes are lower and equal to 0.18 deg, as well as for 53°, 130°, 233°, and 310° axes. The values of perceptive fields have the same order of magnitude as reported by Volbrecht et al (2000) for the L-cone mechanism and for the S-cone mechanism and, by Vassilev et al (2003) in experiments of an incremental or decremental luminance threshold for S-cone 'on' and 'off' signals.

In addition, it was found that the perceptive fields for the stimuli lying along $90^\circ-270^\circ$ axes do not show statistical differences between themselves, according to Vassilev et al (2003), who have shown a larger area of complete summation for S-cone 'off' than for S-cone 'on' stimuli but only at the retinal periphery, while no difference has been found in the central fovea.

In the present study we tested another hypothesis: the extent of an adaptation luminance influence on spatial summation. We also analysed whether the presentation time of the stimulus and the quality of the retinal image contribute to determining the size of Ricco's area. Our results indicate that, in the range from 5 to 40 cd m^{-2}, the adaptation luminance affects the size of the perceptive fields. On average, the perceptive field at 40 cd m^{-2} is 15% smaller than the perceptive field at 5 cd m^{-2}. In general, perceptive fields are larger at lower illuminance levels, and decrease in size as the retinal illuminance is increased (Abramov et al 1992; Sceniak et al 1999; Pitts et al 2005; Troup et al 2005). Considering a range of retinal illuminance (measured in troland—td = cd m^{-2} mm^{2}) from mesopic to photopic values, 0.3log (td) to 3.3log (td) (corresponding to a range of adaptation values from 2.5 to 25 cd m^{-2} approximately), Pitts et al (2005) and Troup et al (2005) found that the perceptive fields depend on retinal illuminance, so that they become bigger as the retinal illuminance decreases, and Abramov et al (1992) showed that the perceptive field of any mechanism is smaller with a white surround. However, Brindley (1954) demonstrated that when the stimuli are presented on a white background, Ricco's area does not change with the adaptation luminance. It is important to note that there are differences between the experiments carried out by Pitts et al (2005) and Troup et al (2005). Pitts et al (2005) took measurements after a 30 min dark adaptation when rods were contributing to the measurements, and they stated that, with increasing retinal illuminance, the perceptive field sizes became smaller owing to reduced rod input. Nevertheless, Troup et al (2005) took measurements after a rod-bleach and showed that perceptive fields become smaller with increasing retinal illuminance. The size of the perceptive fields in a rod-bleach condition decreases from 80% to 100% when the retinal illuminance increases from 0.3log (td) to 3.3log (td). The comparison of the results given by the last two studies shows that the perceptive field sizes reported by Pitts et al (2005) are larger than the ones found by Troup et al (2005); that is, the perceptive fields are larger in the no-bleach condition than in the rod-bleach condition. Obviously, the smaller perceptive fields found by Troup et al (2005) cannot be attributed to the reduced rod input. Not only cones but also rods affect perceptive field sizes at the lowest adaptation luminance. Although rod input is an important factor, the behaviour of the perceptive field as a function of adaptation luminance cannot be explained simply in terms of rod signals and is probably attributable to a cone-based mechanism (see Troup et al 2005). This discussion suggests that rods are being dismissed as a factor. The properties of the colour processing system mediate this intensity change, but another mechanism may be involved, like cone photoreceptor densities and distributions, as well as spatial summation factors (Troup et al 2005), and perhaps something similar to that shown physiologically by Sceniak et al (1999). In our case, there is no rod contribution because, according to the data reported by Curcio and Allen (1990), in the fovea the rod-free zone includes an area of 1.25°, which is bigger than the size of the stimuli involved in our experiment. It is unlikely, therefore, that the rods affect the results at 5 cd m^{-2}. For this reason, the small difference in size of the perceptive fields found with adaptation luminance could be attributed, in accordance with Troup et al (2005), to a cone-based mechanism, not to the rod intrusion.

Another interesting problem is the validity of the correlation between the perceptive and receptive fields at several levels along the visual pathway, because different correlations could be made between these types of fields. According to Pitts et al (2005) it is unlikely that the neural origin of the perceptive field depends on stimulus intensity; therefore this comparison is not valid. It would be interesting to know if the variability of the perceptive fields is a consequence of the method or is there a physiological substrate. It should be noted that the experiments carried out by Pitts et al (2005) and Troup et al (2005) differ from those presented here. These authors carried out experiments on colour appearance; therefore it is possible that the chromatic perceptive fields measured are cortically based as postulated by Abramov et al (1991); this could warrant more research.

The presentation time of the stimulus is also a significant variable. Ricco's area decreases when the stimulus duration increases, since the presentation time can cause movements of the eye during an attempted gaze fixation. There is a tendency for Ricco's area to become smaller at a longer presentation time, greater than 400 ms, but this effect is too small to be statistically significant (Vassilev et al 2005). In our case, the presentation time was fixed at 300 ms. Although the total time of the stimulus is 900 ms, it reaches the threshold purity excitation after 300 ms, the constant part of its temporal configuration. The same occurs in the last 300 ms. Therefore, it is unlikely that this variable could affect our results.

The quality of the retinal image contributes to determining the size of Ricco's area (Ogle 1961; Davila and Geisler 1991). Thus, since in our case the stimulus presents blurred borders, the perceptive field could depend on the way in which its size is quantified through the standard deviation. The chromatic aberration blurs the short-wavelength stimuli that would affect the detection threshold, especially the small stimuli and therefore the spatial summation curve. Therefore, the value of the perceptive field can differ from the values that result from a different stimulus configuration, as in the case of the works mentioned earlier (Volbrecht et al 2000; Vassilev et al 2003).

The present findings may have some practical implications. The most obvious among them is the possibility that, when the experimental RMS_i data points are insufficient, the area of complete summation could be evaluated simulating the data using the previously proposed exponential function and then fitting these data by a bilinear function (Ricco's law and Piper's law).

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