

# Cone weights for the two cone-opponent systems in peripheral vision and asymmetries of cone contrast sensitivity

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## Abstract

In understanding the basis of the changes in human color vision across eccentricity, one key piece of information remains unknown, whether the relative cone weights of the two cone opponent mechanisms vary. Here we measure detection threshold contours within three planes in a 3-dimensional cone contrast space to reveal the L, M and S-cone weights to the two cone opponent mechanisms, L/M and S/(L + M). We find these remain constant across eccentricity suggesting the underlying structures of the cone opponent mechanisms are invariant. The contrast sensitivities of two poles of the S-cone opponent mechanism also remain symmetrical, whereas small asymmetries develop in L/M opponency from about 15°.

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## 1. Introduction

Human color vision is based on two cone-opponent systems, loosely called ‘red–green’ and ‘blue–yellow’. The red–green system responds to the difference between long-wavelength-sensitive (L) cone responses and middle-wavelength-sensitive (M) responses ( $aL - bM$ ), while the blue–yellow system differences short-wavelength-sensitive (S) cones with a combination of L and M cones ( $aS - (bL + cM)$ ). The relative cone weights for each of these two postreceptoral mechanisms have been estimated for foveal vision from measurements of detection threshold contours in a color space and noise masking (Chaparro, Stromeyer, Kronauer, & Eskew, 1994; Cole, Hine, & McIlhagga, 1993; Eskew, Newton, & Giulianini, 2001; Giulianini et al., 1998; King-Smith, Vingrys, & Benes, 1987; Sankeralli & Mullen, 1996, 1997; Stromeyer, Chaparro, Tolia, & Kronauer, 1997; Stromeyer, Cole, & Kronauer, 1985). The red–green mechanism, which has been more fre-

quently investigated, has L and M cone inputs in balanced opposition (1L:1M), with possibly a small S-cone input (Cole et al., 1993; Sankeralli & Mullen, 1996; Stromeyer et al., 1998). The blue–yellow mechanism is more variable between subjects and the cone weights are harder to ascertain because of the low contrast sensitivity of this mechanism, but available estimates indicate a S-cone input in balanced opposition to a combination of L and M cone ( $1S - (0.5L + 0.5M)$ ) (Sankeralli & Mullen, 1996, 1997).

There are three types of change that are known to occur in color vision between fovea and periphery. There is a differential loss of cone contrast sensitivity across eccentricity between the red–green and blue–yellow cone opponent mechanisms (Mullen & Kingdom, 2002; Mullen, Sakurai, & Chu, 2005). Contrast sensitivity for red–green cone opponency declines steeply away from the fovea and is no longer measurable, even for the lowest spatial frequencies, by around 25° in the nasal visual field (Anderson, Mullen, & Hess, 1991; Mullen, 1991; Mullen & Kingdom, 1996; Mullen et al., 2005; Stromeyer, Lee, & Eskew, 1992). By contrast, the contrast sensitivity of blue–yellow cone opponency is better maintained across eccentricity, reflecting the distinct physiological origins of the two systems. In

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addition, small differential contrast sensitivity losses have been reported within the red–green cone opponent system, with lower sensitivity to green than to red emerging at 14–20° of eccentricity (Stromeyer et al., 1992; Newton & Eskew, 2003). Equivalent effects in blue–yellow cone opponency have not been investigated. Lastly, it is known that there are marked changes in color appearance with eccentricity; the hues of red and green stimuli shift toward unique yellow while those of blue and yellow stimuli do not change, color desaturation occurs with an increasing eccentricity, and the color zone named as green narrows with respect to red (Abramov, Gordon, & Chan, 1991; Ayama & Sakurai, 2003; Boynton, Schafer, & Neun, 1964; Gordon & Abramov, 1977; Sakurai, Ayama, & Kumagai, 2003). These changes in color appearance are likely to be influenced by the differential losses in contrast sensitivity both between and within the two cone opponent systems, but these links have not yet been specifically explored.

In understanding the basis of the changes in human color vision across eccentricity, one key piece of information remains unknown, whether the relative cone weights of the two cone opponent mechanisms vary. Changes in the cone weights, reflecting changes in the structure of the cone opponent processes, would have a number of important effects and would potentially influence changes in color appearance and contrast sensitivity with eccentricity. From a practical point of view, the selection of cardinal stimuli that isolate the cone opponent mechanisms also relies on quantitative knowledge of the cone opponent mechanisms. The aim of this paper is two-fold. First, we aim to determine the cone weights of both cone opponent mechanisms in the periphery. This issue has been addressed in a previous study, but only using a 2D color space based on the L and M cone responses and so excluded the S-cone contributions to cone opponency (Newton & Eskew, 2003). Here we specifically include the blue–yellow cone opponent mechanism, as well as the S-cone contribution to the red–green mechanism. We measure detection threshold contours in three different planes in a 3-dimensional cone contrast space, selected to reveal the cone weights to the two cone opponent mechanisms: the L/M plane, which reveals the L and M cone inputs to the red–green mechanism; the isoluminant plane  $(L - aM)/S$ , which reveals any S-cone input to the red–green mechanism; and the  $(L + M)/S$  plane, which reveals the S-cone weights relative to the L and M in the blue–yellow cone opponent mechanism. Since we know that color contrast sensitivity is lost relative to luminance contrast sensitivity in the periphery, we used luminance masking noise (dynamic, 2-dimensional) to suppress the contribution of the luminance system to detection threshold and so producing elongated detection threshold contours that better reveal the peripheral chromatic responses. Changes in the relative cone weights between fovea and periphery are revealed by a change in the orientation of the detection threshold ellipses.

Our second aim is to explore the asymmetries in detection threshold between the two poles of each cone opponent mechanism across the visual field. This has not been mea-

sured systematically across eccentricity for red–green cone opponency, and has not been tested at all for the blue–yellow mechanism. Asymmetries for the blue–yellow cone opponent mechanism are possible since there is evidence that S-cone ON and OFF visual pathways have psychophysical differences in spatial summation and arise from physiologically distinct subcortical neurons (Shinomori, Spillmann, & Werner, 1999; Vassilev, Zlatkova, Manahilov, Krumov, & Schamberger, 2000; Chatterjee & Callaway, 2003; Vassilev, Mihaylova, Racheva, Zlatkova, & Anderson, 2003). Furthermore, if the asymmetry in contrast sensitivity reported for red–green cone opponency (Newton & Eskew, 2003; Stromeyer et al., 1992) is connected to variations in macular pigmentation, we might expect an asymmetry in the blue–yellow cone opponent mechanism bigger than that found for red–green. To address this issue, we tested cone contrast sensitivity for rectified blue, yellow, red and green, cardinal stimuli across eccentricity, and used a correction for the loss of macular pigment density with eccentricity. Since we are testing for asymmetries in detection thresholds between opposite directions in the plane (eg. red vs. green), we used a rectified stimulus (Gaussian), and measured thresholds independently in each direction. To optimize contrast sensitivity this stimulus, presented in the horizontal meridian, was scaled by the magnification factor by vertical elongation since this better confines it in eccentricity than a round stimulus scaled in both horizontal and vertical dimensions.

## 2. Methods

### 2.1. Stimuli and color space

All stimuli were elongated Gaussian “blobs” on a grey background. The standard deviation of the Gaussian envelope was fixed (0.5°) in the horizontal meridian, but varied in the horizontal meridian from 0.5° at 0° of eccentricity to 0.5°, 0.9°, 1.4°, and 1.8° at 5°, 10°, 15°, and 20° of eccentricity, respectively, determined by the magnification factor in V1 (Horton & Hoyt, 1991). A temporal Gaussian envelope was used (Standard deviation = 0.125 s). All stimuli were presented in the centre of the CRT display with a fixation dot positioned for eccentric viewing of the stimulus in the nasal field.

For measurements of detection threshold contours, test stimuli were used from at least eight different directions in each of the three planes (L/M,  $(L - aM)/S$  and  $(L + M)/S$ ), where  $a$  represents the L:M cone ratio of the luminance mechanism as determined for each subject. To suppress the increased contribution of the luminance mechanism relative to the chromatic mechanisms in peripheral vision, high contrast achromatic masking noise was interleaved with each stimulus frame for the L/M and  $(L + M)/S$  planes at eccentric viewing; noise was white, 2-dimensional, dynamic, set to the display contrast maximum (ie. peak Michelson contrast = 50%), and spatially filtered with a low pass Butterworth filter with a 1 cpd cut off. Achromatic masking noise was not required for the isoluminant plane. Stimuli were presented in the fovea and at 20°, except for those in the L, M plane, which were presented at 15° because red–green contrast sensitivity was too low to obtain thresholds at higher eccentricities.

For measurement of the asymmetry between two poles of each cone-opponent system, four test stimuli were used to activate each pole of the two cone-opponent mechanisms in isolation (red, green, blue, and yellow). The cardinal blue and the yellow stimuli respectively incremented or decremented S-cones only (+S or –S). The red and the green stimuli incremented and decremented the L and M cones inputs in the cardinal direction for the red–green mechanism (+L, –M for red and –L, +M for green). Cardinal stimuli were used that were both isoluminant and iso-blue–yellow.

Isoluminance (the value  $a$  mentioned above) was determined for each subject and eccentricity using a standard minimum motion paradigm (e.g. Mullen & Sankeralli, 1999). To ensure that the blue–yellow mechanism did not contribute to red–green detection thresholds, which becomes more likely in the periphery where the sensitivity of the blue–yellow mechanism rises relative to the red–green, stimuli were iso-blue–yellow, meaning that they are orthogonal to the estimated blue–yellow mechanism direction ( $S - 0.5(L + M)$ ) in cone contrast space (Mullen et al., 2005). Stimuli were presented from  $0^\circ$  to  $20^\circ$  in  $5^\circ$  steps on the horizontal meridian of the nasal visual field of the right eye.

Stimuli were represented within a 3-dimensional cone contrast space, in which each axis is defined by cone contrast (the incremental stimulus intensity for each cone type to the stimulus normalized by the intensity of the fixed white background). Stimulus contrast is defined as the vector length for the rectified stimuli in cone contrast units. The cone fundamentals of Smith and Pokorny (1975) were used for the spectral absorption of the L, M, and S-cones at  $0^\circ$ . The  $10^\circ$  cone fundamentals of Stockman and Sharpe (2000) were used for stimuli presented at over  $5^\circ$  of the eccentricity since these take into account the loss of macular pigment with eccentricity (Newton & Eskew, 2003). From these data a linear transform was calculated to specify the required phosphor contrasts of the monitor for given cone contrasts.

## 2.2. Apparatus and calibration

Test stimuli were displayed on a CRT monitor (Mitsubishi Diamond Pro 2070SB, 120 Hz frame rate,  $54 \times 41^\circ$ ) driven by a VSG 2/5 graphics board (Cambridge Research Systems) in a Pentium PC computer. The red, green, and blue phosphors of the monitor were calibrated using a Photo-Research PR-605-PC SpectralScan. The monitor was gamma corrected in software with lookup tables using luminance measurements obtained from an Optical gamma correction system interface with the VSG display calibration software (Cambridge Research Systems). The steady background gray was  $49.7 \text{ cd/m}^2$ ,  $(x, y) = (0.275, 0.293)$ , viewed in a dimly lit room at a distance of 40 cm.

## 2.3. Procedure and subjects

Contrast thresholds were measured using a two alternative forced choice (2AFC) staircase procedure with audio feedback. Stimulus contrast was raised by 25% following an incorrect response, and lowered by 12.5% following two consecutive correct responses. The threshold value was calculated as the mean of the last five reversals of the staircase (81.6% correct level). Staircases were repeated at least 3–4 times to obtain a mean and standard deviation.

Six subjects were used (four females and two males). All had normal color vision. Two subjects were the authors and the others were naïve for the purposes of this study. Three of these subjects were used for the measurement of the detection threshold contours and all six subjects participated in the measurement of the asymmetries between the two cone opponent poles.

## 3. Results

Fig. 1a–c shows the results for the measurement of the detection threshold contours in fovea and periphery, in all three planes, for three subjects. Results of the fits are given in Table 1. Fig. 1a shows results for the L/M plane, selected to reveal the relative L and M cone weights to the red–green cone opponent mechanism in the fovea (red circles) and at  $15^\circ$  (blue triangles). The detection threshold contours are represented by the best-fitting ellipses at each eccentricity. The elongated nature of the peripheral ellipse is enhanced by the use of luminance masking noise and allows a more reliable fit of the minor axis to be made. The peripheral ellipse is expanded compared to the foveal one

indicating an overall loss in contrast sensitivity with eccentricity. A difference in orientation between foveal and peripheral ellipses indicates an eccentricity dependent change in cone weights. Table 1 gives the orientation of the minor axis of each ellipse in each subject. Average orientations across three subjects are  $45.73 \pm 0.47^\circ$  (fovea) and  $45.14 \pm 1.10^\circ$  (periphery), showing no change in ellipse orientation between fovea and periphery. This indicates that a cone opponent mechanism with equal weights of L and M cones determines threshold in the periphery, the same as in the fovea. Our results support previous foveal results obtained with similar methods (Sankeralli & Mullen, 1996).

Results for the isoluminant plane ( $L - aM$ )/S, selected to reveal an S-cone input to the red–green mechanism, at  $0^\circ$  (circles) and  $20^\circ$  (squares) are shown in Fig. 1b. Elevation of the minor axis indicates an S-cone contribution to the red–green mechanism, and a vertically oriented ellipse indicates no S-cone input. Average elevations across the three subjects are small at  $0.72 (\pm 1.24)^\circ$  in the fovea and  $2.01 (\pm 4.14)^\circ$  in the periphery (Table 1). This indicates that the S-cone input to red–green system is very small regardless of the eccentricity. Similar low values have been reported for the fovea (Sankeralli & Mullen, 1996). We note that subject KTM shows a marked asymmetry for thresholds along the +S and –S cone axis and has higher S cone thresholds (note the axis re-scaling).

The  $(L + M)$ /S plane was selected to reveal the S relative to the L and M cone contribution to the blue–yellow mechanism, with results for  $0^\circ$  (circles) and  $20^\circ$  (squares) shown in Fig. 1c. Elevation of the minor axis of the ellipse by  $-55^\circ$  indicates a blue–yellow mechanism with perfectly balanced weights between S-cone and combined L and M cone inputs. The ratio of L and M cone inputs to the ‘yellow’ pole of the blue–yellow mechanism is indeterminate within this plane. The average elevation of the minor axis for the three subjects is  $-38.89 (\pm 6.32)^\circ$  in the fovea, and  $-51.16 (\pm 4.46)^\circ$  at  $20^\circ$  in the periphery (Table 1). This difference is not significant under a two-tailed  $t$ -test suggesting no significant difference between fovea and periphery. This conclusion is supported by the results of previous foveal estimates using three different subjects and similar methods found an average orientation of  $50 \pm 4.8^\circ$  (Sankeralli & Mullen, 1996).

Asymmetries between the two poles of each cone opponent mechanism are investigated in Fig. 2, which shows cone contrast sensitivity plotted as a function of eccentricity for red, green, blue, and yellow cardinal stimuli for six subjects. For all subjects, the sensitivities of red and green stimuli decrease rapidly with eccentricity while the sensitivities of blue and yellow stimuli slightly decrease or remain constant in the peripheral visual field. This differential loss of red/green over blue/yellow cone opponency supports previous results obtained using modulated (AC) stimuli (gabor or sinewave rings) (Mullen & Kingdom, 2002; Mullen et al., 2005). In five of the six subjects (Fig. 2a–d, and f), a red–green asymmetry is observed in peripheral vision at  $15^\circ$  or  $20^\circ$  with the reduction in contrast sensitivity to the green stimulus greater than to the red. In contrast, no

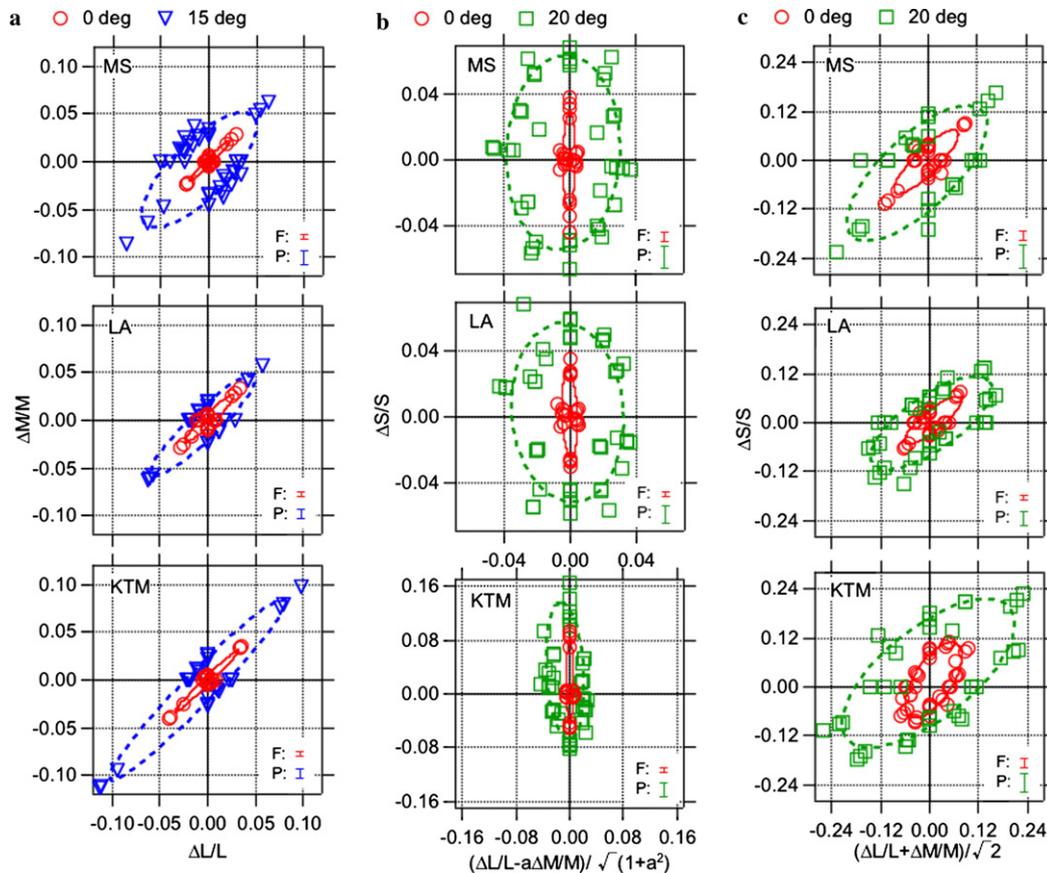


Fig. 1. Detection threshold contours in three planes (columns a–c) of cone contrast space for three subjects. (a) L/M plane at 0° (red circles) and 15° (blue triangles) for three subjects. The detection threshold contours are given by the best-fitting ellipses at each eccentricity. (b) Isoluminant plane ( $L - aM$ )/S at 0° (red circles) and 20° (green squares). Note that the  $x$  axis is scaled for unit length in the isoluminant red–green direction in cone contrast space, and this direction is variable between subjects depending on their isoluminant point. (c)  $(L + M)$ /S plane at 0° (red circles) and 20° (green squares). Each data point shows the average of at least three measurements. Averaged standard deviations are shown for each subject in fovea (F) and periphery (P). Abscissas in (b) and (c) are scaled for unit length.

blue–yellow asymmetry is found systematically in peripheral vision. Subject KTM, as shown Fig. 1, has a consistently higher sensitivity to the yellow than the blue stimulus, but this is found at all retinal locations, and may be due to the effects of age on the optic media, which have not been corrected (Schefrin, Werner, Plach, Utlaut, & Switkes, 1992).

We performed an analysis of variance (one-way ANOVA,  $\alpha = 0.05$ ) on the cone contrast sensitivity for each stimulus condition (red vs. green and blue vs. yellow) for each eccentricity for each subject with significant differences ( $p \leq 0.05$ ) marked by an asterisk (\*). Significant differences are obtained between red and green sensitivities at 10–20° in five of the six subjects (Fig. 1a–d, and f) while for blue and yellow sensitivities significant differences only occur twice, except for subject KTM as noted above.

#### 4. Discussion

##### 4.1. Selective asymmetries in cone contrast sensitivity of the cone opponent mechanisms in peripheral vision

While two previous studies have reported asymmetries in red versus green contrast detection thresholds in the

periphery (Newton & Eskew, 2003; Stromeyer et al., 1992), the blue–yellow results are novel. For red–green cone opponency, we find a small but significant asymmetry of cone contrast sensitivity emerges between 10° and 20° in the nasal field in five of our six subjects with red contrast sensitivity greater than green. Across the population of six subjects our average difference in sensitivity at 20° is a factor of 1.3. Our results are compared with previous results in Table 2. An asymmetry of contrast thresholds was first reported by Stromeyer et al. (1992) on two subjects using red and green 2° flashes of fixed size on a yellow background and assuming an L/M cone opponent contour with equally weighted cone inputs. Green sensitivity was 2× below red at 21°. In a more detailed study, also of two subjects, Newton and Eskew (2003) used 2° flashes of fixed size, corrected for macular pigment, and fitted the sections of the threshold contours to determine the cone weights. An average red–green difference of 1.5× was found at 18°. Here we have used macular pigment corrections, scaled our stimuli with eccentricity, fitted threshold contours, and used a larger population of six subjects. The use of larger, spatially scaled test stimuli and/or the inclusion of more subjects (one subject showed no effect) may be causal in reducing

Table 1  
Normalized cone weights for each cone-opponent mechanism are estimated from the minor axes of the relevant contours at each eccentricity (Fig. 1)

Cone-weight estimation						
Subject	Ecc (°)	Azimuth (°)	Elevation (°)	Normalized cone-weight		
				L	M	S
<i>Red–green</i>						
MS	0	–45.23	0.00	0.70	–0.71	—
MS	15	–45.06	0.00	0.71	–0.71	—
LA	0	–46.17	0.00	0.69	–0.72	—
LA	15	–46.28	0.00	0.69	–0.72	—
KTM	0	–45.78	0.00	0.70	–0.72	—
KTM	15	–44.09	0.00	0.72	–0.70	—
Average	0	–45.73 ( <i>SD</i> = 0.47)	—	0.70	–0.72	—
	15	–45.14 ( <i>SD</i> = 1.10)	—	0.71	–0.71	—
<i>S input to RG</i>						
MS	0	–59.00	0.00	0.52	–0.86	0.00
MS	20	–57.75	–2.72	0.53	–0.84	–0.05
LA	0	–80.25	2.15	0.17	–0.98	0.04
LA	20	–83.50	4.95	0.11	–0.99	0.09
KTM	0	–73.50	0.00	0.28	–0.96	0.00
KTM	20	–73.50	3.80	0.28	–0.96	0.07
Average	0	—	0.72 ( <i>SD</i> = 1.24)	—	—	0.01
	20	—	2.01 ( <i>SD</i> = 4.14)	—	—	0.04
<i>Blue–yellow</i>						
MS	0	45.00	–45.08	0.50	0.50	–0.71
MS	20	45.00	–46.23	0.49	0.49	–0.72
LA	0	45.00	–39.14	0.55	0.55	–0.63
LA	20	45.00	–54.92	0.41	0.41	–0.82
KTM	0	45.00	–32.45	0.60	0.60	–0.54
KTM	20	45.00	–52.32	0.43	0.43	–0.79
Average	0	—	–38.89 ( <i>SD</i> = 6.32)	0.55	0.55	–0.63
	20	—	–51.16 ( <i>SD</i> = 4.46)	0.44	0.44	–0.78

L, M, and S-cone directions in cone contrast space correspond to the *x*, *y*, and *z*-direction in a three-dimensional space, respectively. The azimuth is the orientation in L/M plane and the elevation is the orientation in (L, M)/S plane. Cone weights are normalized for unit vector length (stimulus contrast).

the size of the asymmetry, but it still remains significant. In contrast, we find no eccentricity dependent asymmetry in the blue–yellow system, revealing an effect selective to L/M cone opponency, and so indicative of its underlying cause.

Previous literature raises two possible causes for chromatic red–green threshold asymmetries in the periphery. The first is that it is an adaptation of the visual system in response to the presence of macular pigment in the fovea, as proposed by Hibino (1992) in the context of hue cancellation. Macular pigment filters green more than red light and so will tend to depress cone responses to green light over red in the fovea. The reduction in green cone contrast sensitivity in the periphery, albeit only by a small amount, may reflect a means of normalizing (reducing) the green cone contrast response in the absence of macular pigment in peripheral retina compared to its presence in the fovea. There are two arguments against this idea. Macular pigment is extinct by around 5–8° from the fovea (Polyak, 1941) whereas the red–green asymmetry in thresholds only emerges further out at around 14–15°. In addition, one would expect such an effect to also be manifest in the blue–yellow system, since this should be more strongly influenced by the presence or absence of macular pigment. Interestingly, we do not find asymmetries in the blue and yellow cone contrast sensitivities as a function of eccentricity, even

in the region of retina (0–8°) most likely to be affected. Literature based on incremental thresholds and hue cancellation has proposed that the blue–yellow opponent system compensates for variation in macular pigment density whereas the green–red does not (Hibino, 1992). These incremental threshold data, however, are not directly comparable to the cone contrast sensitivities reported here because increment thresholds, in units of stimulus light intensity, do not take into account the Weber response (von Kries adaptation) of cones. Our measurements of cone contrast take into account the effect of macular pigment on the adapting background as well as the test increment, and because macular pigment modulates the intensity of both, cone contrast sensitivity remains relatively robust in the presence of macular pigment. Incremental threshold measurements, on the other hand, correct only for the effects of macular pigment on the increment intensity of the test stimulus and so report much stronger effects of macular pigment density. Stability in the presence of variations in mean chromaticity and intensity is one of the key advantages of the fact that cones respond to contrast. Although adaptive changes to macular pigment density in the two cone opponent pathways may be manifest in other contexts, such as in color appearance, we find that there is no strong evidence for them in cone contrast sensitivity measurements.

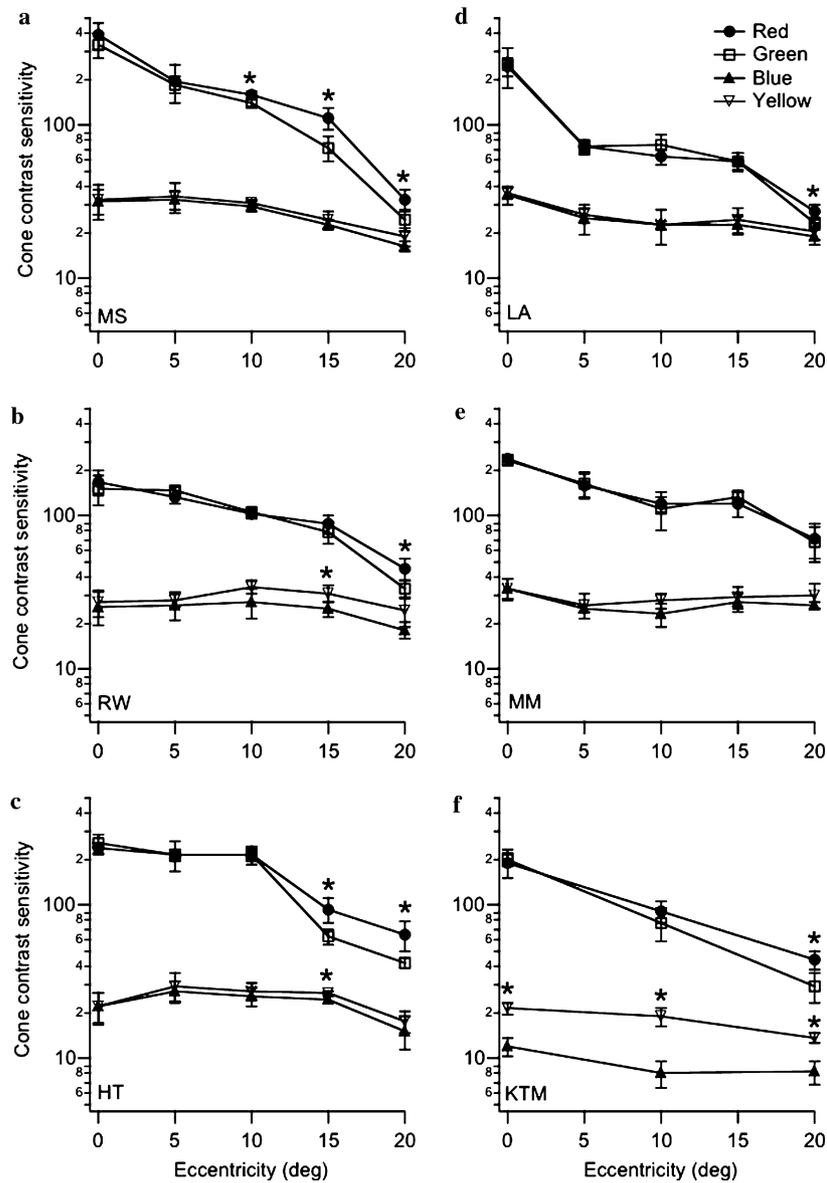


Fig. 2. Change in cone contrast sensitivity for all the stimuli as function of the eccentricity. The symbols represent the average value for each subject. Each panel shows the results of each subject. \* indicates that there is a significant difference between the two plotted contrast sensitivities. Each data point shows the average of at least four measurements.

Another argument for red–green asymmetries has invoked changing proportions of L and M cones in favor of the L cone across eccentricity (e.g. Newton & Eskew, 2003). This has the advantage of accounting for the lack of asymmetry in the blue–yellow mechanism. There are certainly large individual differences in the L/M cone ratio, although the extent of any change as a function of eccentricity remains controversial (Albrecht, Jagle, Hood, & Sharpe, 2002; Brainard et al., 2000; Hagstrom, Neitz, & Neitz, 1998; Krauskopf, 2000; Kremers et al., 2000; Kremers, Stepien, Scholl, & Saito, 2003; Roorda & Williams, 1999). The accumulated evidence, however, including that presented here, demonstrates that the L/M cone opponent mechanism is inherently robust to variations in L:M cone proportions. Moreover, it has been observed that cone proportions do

not affect color phenomena such as the setting of unique yellow (Brainard et al., 2000; Otake & Cicerone, 2000). There may be a simple explanation for this robustness. Assuming opponent units with centres and surrounds that are approximately balanced, the L/M cone opponent response retains equal net L and M cone weights, even for units with single cone centres and mixed cone surrounds that reflect unequal retinal cone proportions.<sup>1</sup> On the other hand, when cone summing (luminance) mechanisms, as

<sup>1</sup> For example, assume a cone population of 3 L:M, and an opponent unit with a single cone centre and mixed surround, balanced between centre and surround. An L-on unit has a cone opponent value of  $(L - 1/4(3L + M))$  or  $1/4L - 1/4M$  and an M-on unit has a cone opponent value of  $(M - 1/4(3L + M))$  or  $3/4M - 3/4L$ , both reflecting equal L/M cone weights.

Table 2  
Thresholds in cone contrast units for 'red' and 'green' stimuli that selectively activate the L/M cone opponent mechanism at detection threshold obtained from this study and the two previous studies

Paper	Eccentricity (°)	Threshold				G/R	No. of subjects
		Red	SD	Green	SD		
Stromeyer et al. (1992)	8	0.0169		0.0185		1.09	1
	14	0.0296		0.0462		1.56	1
	21	0.1359		0.2649		1.95	2
Newton and Eskew (2003)	0	0.0035		0.0052		1.50	1
	18	0.0096		0.0147		1.53	2
Present study	0	0.0043	0.0009	0.0044	0.0008	1.01	6
	10	0.0094	0.0040	0.0098	0.0035	1.04	6
	20	0.0242	0.0085	0.0319	0.0108	1.32	6

G/R shows the ratio of green to red thresholds obtained.

opposed to cone balancing mechanisms, are involved, variations in cone ratios are apparent psychophysically, for example as in the setting of the isoluminant point or in flicker photometric measurements. For these reasons we think that variations in cone proportions are unlikely to be directly responsible for the chromatic red–green peripheral asymmetry.

This red–green asymmetry is probably reflected in the properties of color zone maps (Ikeda, Sekiguchi, & Shioiri, 1985; Sakurai et al., 2003; Takase, 1997), which represent how much the strengths of redness, yellowness, greenness, and blueness are perceived across eccentricity. One of the common properties of the color zone maps is an eccentricity dependent narrowing of the color zone map for the naming of green.

Sankeralli and Mullen (2001) proposed that cone opponent mechanisms are rectified as opposed to bipolar based on an asymmetry of noise masking between the two poles of each opponent mechanism (e.g., red noise fails to mask a green test and vice versa). Unequal sensitivity to increments and decrements, in the absence of any pre-receptorial differential effects, also supports the idea of rectified chromatic mechanisms. Newton and Eskew (2003) suggest that this asymmetry may originate at a cortical level in double opponent cells, and this would also fit with the requirement of a rectified mechanism.

#### 4.2. Cone weights of chromatic mechanisms in peripheral vision

We fitted detection threshold contours in 3 different planes of the cone contrast space in order to estimate the L and M cone weights of the red–green mechanism, the S-cone input to the red–green mechanism, and the S versus L and M cone weights of the blue–yellow mechanism across eccentricity (Table 1). In the fovea, our results for the L and M cone weights agree with those of previous studies showing balanced opponent inputs of L and M cones (Cole et al., 1993; Sankeralli & Mullen, 1996; Stromeyer et al., 1985). We find that these cone weights remain stable across eccentricity (up to 15°), and are also in

agreement with the previous estimate of the peripheral L and M cone weights (Newton & Eskew, 2003). The L and M cone weights of the red–green mechanism are thus remarkably stable both across subject and across eccentricity despite wide individual variations in L:M cone ratios, and possible variation across eccentricity. This stability may be mediated by the presence of balanced opponent centres and surrounds, as described above.

The S-cone inputs to the red–green mechanism and the blue–yellow cone opponent mechanism across eccentricity have not been investigated before. There is known to be a small (0–4%) contribution of S-cones to the red–green mechanism in the fovea although this not present in all subjects (Cole et al., 1993; Sankeralli & Mullen, 1996; Stromeyer et al., 1998). Here we find a weak S-cone input to the red–green mechanism in periphery, which across our three subjects was similar to that in the fovea. Thus overall, these results suggest that the structure of the red–green cone opponent mechanism remains constant across eccentricity.

Our estimates of the S-cone weight relative to the L and M in the blue–yellow mechanism show greater variability than the others, mainly because the major/minor axis ratio is not high. The orientation of this contour (elevation of the minor axis) reflects the relative balance between S and the combined L and M cones, but it cannot reveal the relative weights of L and M cones, which we assume to be equal. The estimates are in agreement with the results of the previous studies at 0° (Cole et al., 1993; Sankeralli & Mullen, 1996), with the latter showing that additional assumptions in the fitting method can affect the estimates of this particular contour by as much as 10°. Overall, our results indicate that the cone weights of blue–yellow mechanism are constant across eccentricity, at least up to 20°, indicating no structural changes within the S-cone opponent mechanism.

In this paper we report that the cone weights of both cone opponent mechanisms remain constant across eccentricity indicating that the underlying structure of the cone opponent mechanisms are invariant. We therefore conclude that the most important change in threshold color vision with eccentricity is the differential variations in the contrast sensitivity of the two mechanisms, mainly in terms of the

greater overall loss of red–green contrast sensitivity compared to blue–yellow (Mullen & Kingdom, 2002; Mullen et al., 2005) but also in terms of the small differential losses between the red and green poles of the L/M cone opponent mechanism, which emerge from about 15°.

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