Perception, 2005, volume 34, pages 951 – 959

DOI:10.1068/p5374

Does L/M cone opponency disappear in human periphery?

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Received 15 June 2004, in revised form 20 December 2004

Abstract. We have assessed the optimal cone contrast sensitivity across eccentricity in human vision of the two cone-opponent mechanisms [L/M or red – green, and S/(L + M) or blue – yellow] and the luminance mechanism. We have used a novel stimulus, termed a 'sinring', that is a radially modulated sine-wave arc, Gaussian enveloped in both angular and radial directions. This stimulus overcomes the problem inherent in Gabor stimuli of confounding stimulus spatial frequency, size, and eccentricity and so allows contrast sensitivity to be tracked accurately into the periphery. Our results show that L/M cone opponency declines steeply across the human periphery and becomes behaviourally absent by 25 – 30 deg (in the nasal field). This result suggests that any L/M cone-opponent neurons found in primate peripheral retina beyond this limit are unlikely to be significant for colour contrast detection measured behaviourally.

1 Introduction

Human colour vision is supported by two cone-opponent mechanisms. One, loosely termed 'red – green', differences the L and M cone responses, whereas the other, loosely termed 'blue – yellow', differences S with a combination of L and M cones.[1] Behavioural work on human colour vision has shown that these two cone-opponent systems have distinctly different distributions of cone contrast sensitivity across the visual field; red – green cone opponency has a high peak in cone contrast sensitivity at the fovea with a steep decline in the periphery, whereas blue – yellow cone opponency has a more even distribution, resembling that for luminance vision (Mullen 1991; Stromeyer et al 1992; Mullen and Kingdom 1996, 2002). As yet there is no clear explanation why there is such a strong foveal specialisation for the red – green system relative to the other two, or where this effect originates.

Curiously, the presence or absence of L/M opponent neurons in the periphery has been hard to establish from single-cell recordings in primates. Martin et al (2001) reported the presence of a high proportion of ganglion cells sensitive to red – green modulation far out in the periphery (20 – 50 deg) of macaque retina. On the other hand, Diller et al (2004) reported that peripheral ganglion cells of macaques are non-opponent at these eccentricities. These findings are in interesting juxtaposition with the marked decline of human L/M cone contrast sensitivity in the periphery reported psychophysically. In this paper, we aim to shed light on the role of peripheral L/M cone opponency revealed by primate single-cell recording by establishing the presence or absence of L/M cone opponency behaviourally in the human periphery. Previous psychophysical measurements have not been able to do this definitively because they have been limited in the way that chromatic contrast sensitivity in the far periphery was measured. This limitation is the confounding of the stimulus size (a grating patch or spot) and its location in eccentricity. The stimulus spatial frequency must be reduced or spot size increased

[1] We used the colour terms 'red – green' (RG) and 'blue – yellow' (BY) to refer specifically to the two cone-opponent mechanisms. These mechanisms when activated individually by cardinal stimuli do not give rise to the colour sensations of unique red, green, blue, or yellow and so should not be confused with the colour-opponent processes.

to obtain optimal sensitivity as eccentricity increases (Robson and Graham 1981), and thus very large stimuli are required at high eccentricities. Such large stimuli are, by definition, not well localised in eccentricity, and may be detected by the region lying closest to the fovea so confounding the accurate determination of sensitivity in the periphery.

To overcome this problem and establish the presence or absence of red–green cone opponency in the periphery we have designed a new stimulus for which spatial frequency and eccentricity are not confounded. This is a sine-wave ring stimulus (termed 'sinring') illustrated in figure 1, Gaussian-enveloped to form an arc, in which spatial frequency is determined by an angular modulation, thus maintaining a constant distance (eccentricity) from the fovea for all spatial frequencies regardless of their spatial extent. We measured optimal cone contrast sensitivity for the two chromatic mechanisms and the luminance mechanism as a function of eccentricity to determine their decline with eccentricity.

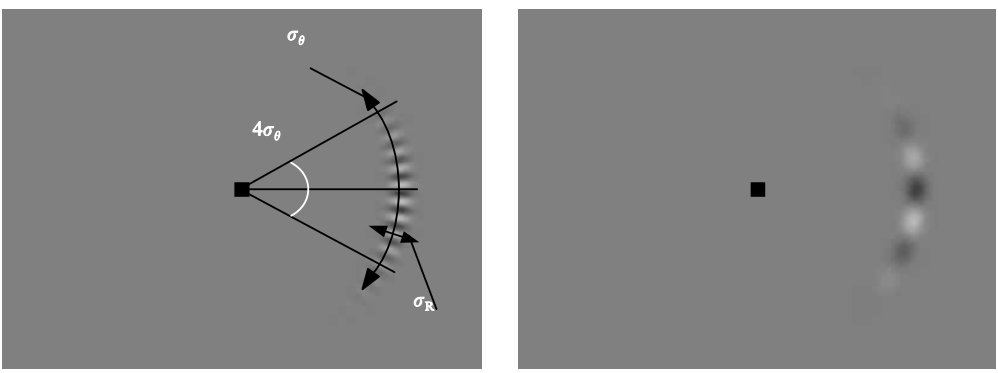

Figure 1. Examples of the 'sinring' stimulus consisting of a sine-wave ring pattern defined in polar coordinates. Contrast is Gaussian-modulated in both radial and angular directions (σ_R = radial space constant, σ_θ = angular space constant). The example spatial frequency for the left panel is 0.5 cycle deg^{-1} and for the right panel 0.125 cycle deg^{-1} viewed at 20 deg of eccentricity. A fixation point was present throughout, and changed from circular to square during display trials. A colour version of this figure can be viewed on the *Perception* website at http://www.perceptionweb.com/misc/p5374/.

2 Methods

2.1 *Stimuli*

The stimuli used were sine-wave ring patterns defined in polar coordinates (r, θ) and consisting of angular sinusoidal modulation presented in an annulus with Gaussian envelopes modulating contrast in both radial and the angular directions (figure 1).

The annular segments $s(r, \theta)$ were obtained by multiplying a Gaussian patch $g(r, \theta)$ and an angular sinusoidal modulation $m(\theta)$, given by:

$$g(r,\,\theta) = \exp\left[-\frac{(r-R_0)^2}{2\sigma_R^2}\right]\exp\left[-\frac{(\theta-\theta_0)^2}{2\sigma_\theta^2}\right], \tag{1}$$

$$m(\theta) = \sin(\omega\theta + \theta_p), \tag{2}$$

$$s(r,\,\theta) = L_0[1 + cm(\theta)g(r,\,\theta)], \tag{3}$$

where R_0 is the eccentricity of the stimulus relative to the fixation point, σ_R the radial space constant, θ_0 the angular position of the sector, σ_θ the angular space constant, ω the angular frequency, θ_p the angular phase, L_0 the mean luminance, and c the contrast. In the experiments, spatial frequency refers to the modulation per unit length along the circumference (in cycles per degree) and was variable. The radial space

constant (σ_R) was 0.8 deg for eccentricities of 2 – 15 deg inclusive, and 1.5 deg for eccentricities of 20 – 30 deg. The angular space (σ_θ) constant was 30 deg for stimuli at 2, 5, and 10 deg of eccentricity corresponding to a stimulus arc length of 1, 2.5, and 5 deg, respectively. For 10 – 30 deg, σ_θ was set to maintain a fixed stimulus arc length of 5 deg. Angular sinusoidal modulation of the stimuli also has the benefit of reducing the effects of transverse chromatic aberrations. In addition, the use of very low spatial frequencies in this study for optimal cone contrast sensitivity measurements will reduce the effects of longitudinal aberrations (Bradley et al 1992).

2.2 *Colour space*

The three cardinal stimuli were used, designed to isolate each of the three postreceptoral mechanisms (RG, BY, or Lum). Their chromaticity was defined in a 3-D cone-contrast space in which each axis (termed L, M, or S) represents a cone contrast defined as the quantal catch of the L-, M-, or S-cone types normalised with respect to the white background (Sankeralli and Mullen 1996, 1997). Stimulus chromaticity and contrast are given by the vector direction and magnitude, respectively. The coordinates of the cardinal stimuli in this space were: 1L + 1M + 1S (the achromatic direction, orthogonal to the BY and RG mechanisms), S only (the blue – yellow direction, orthogonal to the RG and luminance mechanisms), and a red – green direction orthogonal to both the BY and luminance mechanisms (isoluminant and iso-blue – yellow). The isoluminant point was determined individually at each eccentricity, spatial frequency, and for each subject by a method of adjustment to define a minimum in perceived motion for a Gabor patch (0.5 – 0.125 cycles deg^{-1} depending on eccentricity) viewed monocularly. As examples, the RG cardinal stimuli used at 2 deg of eccentricity had L, M, and S cone weights, respectively, of $1 : -2.75 : -0.875$ for KTM; $1 : -19.1 : -9.04$ for MS; and 1L : 5.53M : 3.27S for WC.

2.3 *Apparatus and calibration*

Stimuli were displayed on a large Electrohome (Retro III) back-projection CRT monitor measuring 138 cm by 104 cm, driven by a VSG2/5 graphics board (Cambridge Research Systems) with 15 bits contrast resolution housed in a Pentium PC computer. The frame rate of the display was 120 Hz. Mean luminance was 75 cd m^{-2} at screen centre. For the method of chromatic calibration and the gamma linearisation calibration see Mullen and Beaudot (2002).

2.4 *Protocol*

Contrast detection thresholds were obtained by a 2AFC staircase procedure in which contrast was reduced after two correct responses, and increased after one wrong response, corresponding to a criterion of 71% correct responses. Each session was terminated after six reversals, and the detection threshold was computed from the mean of the last five reversals. Data points show the mean of 3 – 5 staircase procedures. Stimulus presentation was Gaussian-enveloped in time with a σ of 83 ms centred in a temporal window of 1 s. Auditory feedback was given after each trial. A black fixation mark was present in the centre of the display as described in the legend of figure 1, and subjects were asked to sustain their fixation during the whole session. Stimuli were presented in the horizontal meridian of the nasal visual field. Three subjects (the authors) were used in all experiments. All had normal colour vision and were optically corrected as necessary.

3 Results

Cone contrast sensitivity was measured as a function of eccentricity (2 to 30 deg in the nasal visual field) for six different spatial frequencies (1, 0.75, 0.5, 0.25, 0.125, and 0.0625 cycle deg^{-1}). Not all spatial frequencies were used at all eccentricities since the higher spatial frequencies typically cannot be seen at the greater eccentricities.

From this data set we determined the spatial frequency that provides optimum cone contrast sensitivity at each eccentricity for each subject, shown in table 1. Note that, owing to the low-pass nature of the colour-contrast sensitivity functions (Granger and Heurtley 1973; Mullen 1985), the spatial frequencies required for optimal chromatic sensitivity are relatively low. Moreover, optimal spatial frequencies shift to lower values with eccentricity for all three mechanisms, reflecting a well-established trend. The combination of these two factors means that optimal contrast sensitivity for the colour systems is typically 0.0625 cycles deg^{-1} by 25 deg of eccentricity. The 'sinring' stimulus has the advantage of allowing such large spatial wavelengths (16 deg) to be displayed without loss of eccentric localisation.

Table 1. The spatial frequencies used at each eccentricity to obtain the cone contrast sensitivity data of figure 2, indicated for each subject. Single values indicate the same spatial frequency was used for each subject.

Eccentricity /deg	Spatial frequency of peak cone contrast sensitivity/cycle deg^{-1}		
	Ach	RG	BY
2	1	0.5	0.25 (MS, WC), 0.5 (KTM)
5	1	0.25 (MS, WC), 0.5 (KTM)	0.25 (MS, WC), 0.5 (KTM)
10	1	0.25	0.25
15	1	0.25	0.25
20	0.5	0.25 (MS), 0.125 (KTM), 0.0625 (WC)	0.25
25	0.75 (MS, WC), 0.5 (KTM)	0.0625	0.25
30	0.5	0.0625 (WC)	0.0625 (MS, WC), 0.125 (KTM)

In figure 2a we plot cone contrast sensitivity across eccentricity for each of the RG, BY, and Ach cardinal stimuli for the optimal spatial frequencies in table 1, on the basis of a new data set. Results show high cone contrast sensitivity to RG stimuli in central vision followed by a steep decline. Cone contrast sensitivities to Ach and BY stimuli fall below those for RG in central vision but have a shallower decline, and by 20–25 deg red–green and luminance cone contrast sensitivities are similar in our three subjects. The dashed line represents the stimulus-bound RG contrast, or the maximum cone contrast that can be achieved in the RG cardinal direction for the red–green stimulus. This limit is determined more by the overlap of the L and M cone spectral sensitivities than by the particular phosphors of the monitor.

We were interested to determine the eccentricity at which L/M cone contrast sensitivity fell to this physical limit. This occurred by 25 deg of eccentricity for subjects MS and KTM, and 30 deg for subject WC. Although the plotted data points lie marginally above the physical stimulus limit (dashed line), this is because threshold protocols require the stimulus to be presented above detection threshold on initial trials. We conclude that L/M cone contrast thresholds have reached their stimulus-bound maximum between 25 and 30 deg of eccentricity.

In order to ascertain that this is the genuine limit of L/M cone contrast sensitivity, we have to establish that our stimuli yield optimal cone contrast sensitivities. One possibility is that an additional number of spatial cycles in the stimulus will increase sensitivity owing to an effect of spatial summation. We performed a control experiment to test this possibility, in which we varied the angular space constant, σ_θ, in order to determine the effect of the number of spatial cycles in the stimulus on cone contrast sensitivity. Results (shown for one subject in figure 2b) indicate that the angular extent of our stimulus is sufficient to obtain optimal levels of cone contrast sensitivity in all mechanisms at the highest eccentricities used.

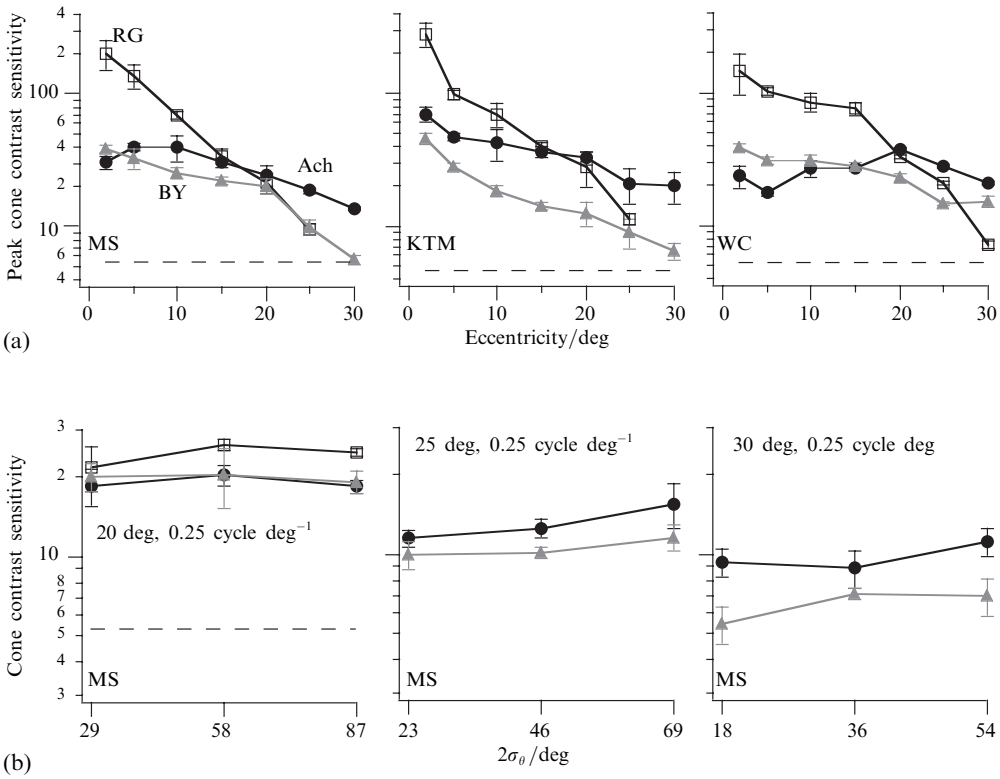

Figure 2. (a) Peak cone contrast sensitivity as a function of eccentricity (2 – 30 deg) for the three cardinal stimuli: achromatic (circles), blue – yellow (triangles), and red – green (squares). Peak cone contrast sensitivity refers to the maximum cone contrast sensitivity obtained from the set of spatial frequencies measured (1, 0.75, 0.5, 0.25, 0.125, and 0.0625 cycle deg^{-1}). The dashed line shows the maximum stimulus contrast for the cardinal RG stimulus. Data are for three subjects. Error bars show ± 1 SD. (b) Results of the control experiment on spatial summation. Cone contrast sensitivity is plotted as the number of spatial cycles in a stimulus of 0.25 cycle deg^{-1} is increased, given by the Gaussian spread of the angular contrast envelope ($2\sigma_\theta$) (the angular space constant of the stimulus). Three eccentricities are shown: 20, 25, and 30 deg. Data shown are for one subject (MS) although three subjects completed the experiment with similar results. Symbols are as used in (a). At 25 and 30 deg the RG stimulus could no longer be seen.

4 Discussion

Our results support previous conclusions obtained with Gabor stimuli that colour-contrast detection by L/M cone opponency is highly sensitive in the fovea but falls steeply across the periphery (Mullen 1991; Stromeyer et al 1992; Mullen and Kingdom 1996, 2002). It is interesting to note that, as a consequence of this steep loss of L/M cone opponency, the three postreceptoral mechanisms become quite well matched in cone contrast sensitivity by 20 – 25 deg, and beyond this eccentricity the luminance system is more sensitive than either chromatic system. These results illustrate the strong specialisation for L/M cone opponent contrast sensitivity in central vision over and above that for luminance or S-cone-opponent contrast sensitivity. Although by 20 – 25 deg the three postreceptoral mechanisms have similar cone contrast sensitivities, the L/M cone-opponent mechanism has reached its stimulus bound contrast limit, and sensitivity cannot be improved by altering the stimulus parameters, such as lowering spatial frequency or increasing stimulus size. Use of the 'sinring' stimulus, which, unlike Gabor stimuli, does not confound stimulus size, spatial frequency, and eccentricity, has enabled the limiting values of L/M cone contrast sensitivity to be determined in the human periphery. A 'stimulus-bound'

contrast limit means that the contrast of the red–green cardinal stimulus is at its maximum and cannot be increased to measure cone contrast sensitivity any further. This limit originates from the high degree of overlap between the L and M cone spectral sensitivities that restricts the amount that they can be differentially modulated. Because this limit is mainly cone-based, the use of different CRT phosphors will not affect it significantly. Thus we conclude that there is little or no L/M cone opponent response measurable psychophysically beyond 25–30 deg of eccentricity in the nasal visual field.

It is worth noting that it requires extremely low spatial frequencies (eg 0.0625 cycle deg^{-1}) to obtain measurable L/M cone contrast sensitivities out to 25 deg of eccentricity. Cone contrast sensitivity for stimuli of higher spatial frequencies will decline more steeply and collapse at lower eccentricities. Thus, for most stimuli, L/M cone opponency is more confined to central vision than these limiting results might suggest. To illustrate this point we have measured the loss in cone contrast sensitivity for a single fixed Gabor stimulus (1.5 cycles deg^{-1}, $\sigma = 0.2$ deg) and used the data to construct the two pictures in figure 3a (red–green) and 3b (achromatic). Each picture shows a field of pseudo-randomly placed Gabor elements in a nominal 10 deg $\times$ 10 deg square patch. Both fields have an overall Gaussian contrast envelope, peaking at the centre, that simulates the contrast sensitivity loss measured psychophysically for the respective biological detection mechanism (shown in the graphs on the right). These simulations demonstrate the high contrast attenuation across the visual field for the L/M system compared to the achromatic.

It is interesting to ask what is the wider significance of the presence or absence of L/M cone opponency in the periphery, and why it has become controversial. The presence of L/M cone-opponent neurons in the periphery that draw on relatively high number of cones is key evidence in favour of selective connections in the retina that guide individual L and M cone types to project exclusively to the centre or surround of a receptive field. If a receptive field draws on large numbers of cones, selective projections are essential to establish cone selectivity in the centre or surround and hence cone opponency. It has been established for decades that a high proportion of L/M cone-opponent neurons are present in primate retina (Wiesel and Hubel 1966; Gouras 1968; Derrington et al 1984). Evidence for cone selectivity, however, requires neurons to be both L/M cone opponent and multi-cone, something which has been established only rarely (Reid and Shapley 1992; Martin et al 2001). This is important because the L/M cone-opponent neurons in the retina are the very small midget cells, confined mainly to the central regions of the visual field, and drawing typically on only one cone in the receptive field centre (Shapley and Perry 1986; Dacey 2000). Under conditions of a few (1–5) cones per receptive field centre, cone opponency could arise by chance, with different proportions of L and M cones occurring in centre and surround regions of the receptive field as predicted from binomial probabilities (Mullen and Kingdom 1996). Thus, only neurons drawing on large numbers of L or M cones can potentially provide evidence in favour of a L/M opponency arising via selective cone projections rather than by chance. Moreover, the mystery is deepened by the fact that the hunt for a mechanism implementing L versus M cone selectivity in the inner or outer retina has so far proved negative (Wässle et al 1989; Calkins and Sterling 1996; Dacey et al 1996).

Clearly our behavioural study cannot resolve this physiological controversy about L/M cone selectivity in the retina. On the other hand, we can determine the behavioural significance of L/M cone opponency in the periphery. The psychophysical experiments reported here have demonstrated the complete loss of L/M cone opponency at the behavioural level by 25–30 deg of eccentricity. This result suggests that the outputs of any L/M cone opponent units responding in the retinal periphery at or beyond these

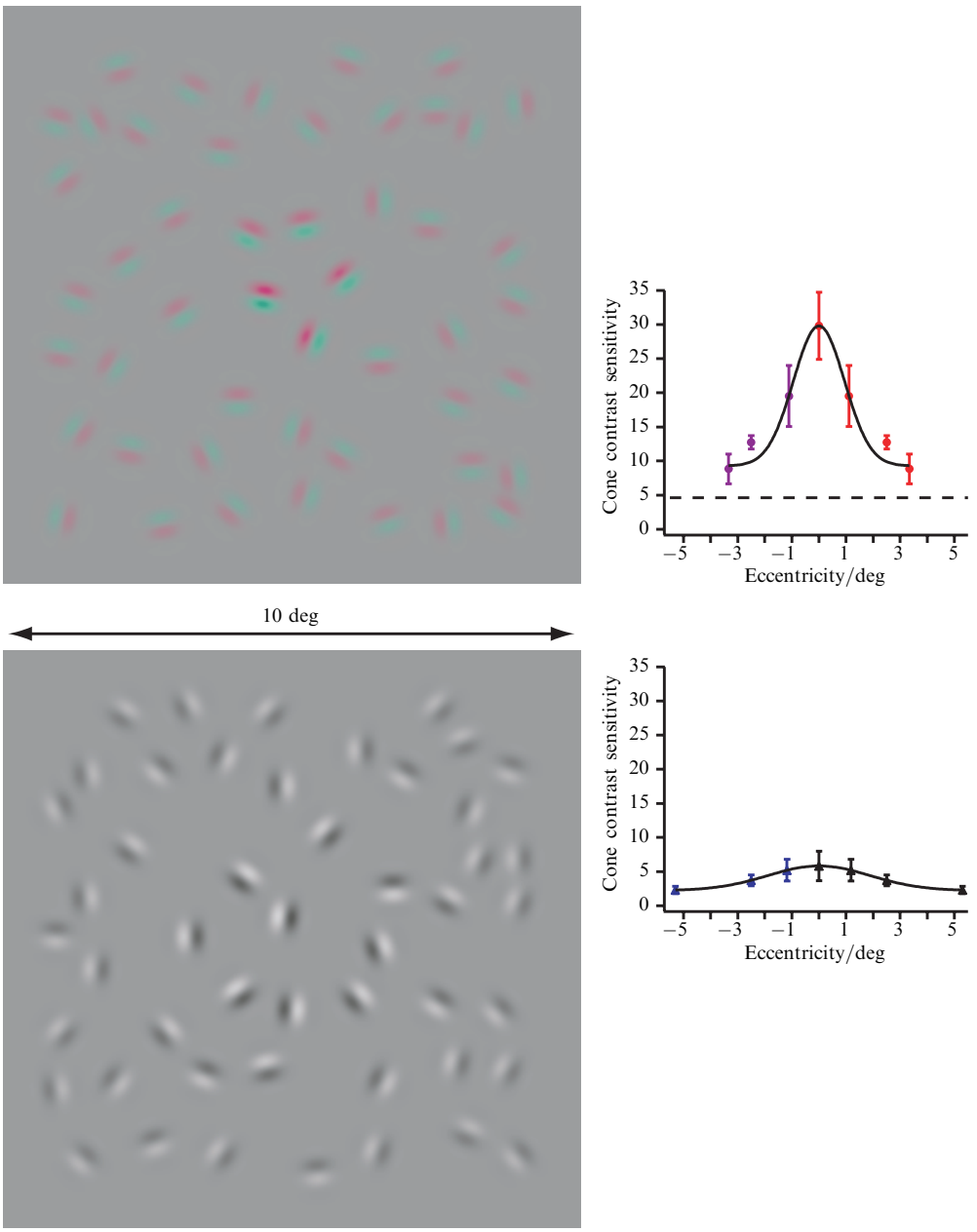

Figure 3. The top and bottom right panels show the cone contrast sensitivities (mean ±1 SD) as a function of eccentricity for a single small Gabor patch (1.5 cycles deg^{-1}, $\sigma = 0.2$ deg), which is either isoluminant RG (top) or achromatic (bottom). Subject KTM. Data are fitted with a Gaussian function. The same Gabors, pseudo-randomly placed, are used in the stimuli figures on the left in a nominally 10 deg × 10 deg square patch. The contrast of this stimulus field has been enveloped in 2-D with the Gaussian obtained from the data fit on the left for the loss in stimulus contrast across eccentricity.

eccentricities are not significant for colour contrast detection but may be used by other mechanisms (Kulikowski et al 1997; Vidyasagar et al 2002).

We should expect that the selective decline in and eventual loss of L/M cone contrast sensitivity would have an effect on colour appearance in the periphery. In general, the hues of red or green stimuli shift towards unique yellow, while those of

blue and yellow do not change, and losses of saturation occur, which are superficially compatible with our results (van Esch et al 1984; Abramov et al 1991; Sakurai et al 2003). On the other hand, particularly with spatially scaled stimuli, hue detection and discrimination has been reported out to further eccentricities than the 25 – 30 deg limit (in the nasal field) that we report for L/M contrast sensitivity (Noorlander and ›Koenderink 1983; van Esch et al 1984; Abramov et al 1991). Our results suggest that, at eccentricities beyond 30 deg, hue appearance will rest only on the activities of the S cone-opponent and the luminance mechanisms, however, this remains to be determined directly.

Finally, the determination of L/M cone opponency in the periphery requires particular care, since the cone contrast sensitivity of the S cone-opponent mechanism is similar to that of the L/M one. It is important to select stimuli that are truly cardinal and eliminate the response of the S cone-opponent mechanism as well as the luminance mechanism. Unless RG stimuli are iso-blue – yellow (orthogonal to the S cone-opponent mechanism in a cone contrast space) as well as isoluminant, RG stimuli may cross-activate the BY mechanism; for example, a red – green stimulus that is isoluminant but not iso-BY (eg 1L : −3M : 0S) will cross-activate the BY mechanism with a contrast at 26% of the stimulus contrast. Hence, use of an iso-BY stimulus is crucial for the successful isolation of the L/M cone-opponent mechanism both physiologically and psychophysically.

Acknowledgments. We are grateful to Dr. W H A Beaudot for his contribution to the stimulus programming. This study was funded by a CIHR grant to author KTM (MOP-10819).

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© 2005 a Pion publication

ISSN 0301-0066 (print) ISSN 1468-4233 (electronic)

PERCEPTION
VOLUME 34 2005

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