Pergamon

0042-6989(95)00261-8

Vision Res., Vol. 36, No. 13, pp. 1995–2000, 1996

Printed in Great Britain
0042-6989/96 $15.00 + 0.00

Losses in Peripheral Colour Sensitivity Predicted from "Hit and Miss" Post-receptoral Cone Connections

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Received 28 August 1992; in final form 28 September 1995

On the basis of the early primate neurophysiological recordings, it was thought that the different cone types of the primate retina project selectively into the centre and surround of the receptive fields of cone opponent neurons, and more recently this view has been reasserted on the basis of physiological results. An alternative idea is that these projections are in fact unselective for cone type, and, therefore, cone opponency arises from chance variations in the proportions of different cone types in centre and surround. The issue is presently controversial with anatomical or physiological support for both hypotheses. Our results show that there is a selective loss of red–green colour sensitivity across the human visual field. Furthermore, this selective loss occurs under low temporal frequency conditions (0.5 Hz) which were selected to favour the mediation of both colour and luminance detection by a common P cell pathway and to exclude an M cell contribution to detection threshold. We show that "hit and miss" post-receptoral cone projections will produce a decline in cone opponency that is sufficient to account for this selective loss, thus providing psychophysical evidence consistent with this hypothesis. Copyright © 1996 Elsevier Science Ltd.

Colour vision Peripheral vision Colour contrast sensitivity Isoluminance Cones

INTRODUCTION

Colour vision degrades continuously across the visual field (Gordon & Abramov, 1977; van Esch *et al.*, 1984; Noorlander *et al.*, 1983; Mullen, 1991; Anderson *et al.*, 1991; Stromeyer *et al.*, 1992). Although sensitivity to both colour and luminance contrast decline with eccentricity, the loss in colour contrast sensitivity is considerably greater (Mullen, 1991; Stromeyer *et al.*, 1992). Furthermore, there is a greater loss in colour compared to luminance spatial resolution across the visual field (Anderson *et al.*, 1991). These factors suggest that the colour loss is selective, and imply that there is an aggregation of chromatic mechanisms relative to achromatic mechanisms within the central visual field.

There are at least three potential sources of variation affecting the relative sensitivity to colour and luminance contrast across the visual field. Firstly, the ratio of M cells to P cells may vary with eccentricity. Since only the P cells display significant chromatic sensitivity, any reduction in the proportion of P to M cells might potentially produce a decline in colour, relative to luminance contrast sensitivity. Whether there is any variation with eccentricity in the proportions of M and P cells is presently a contentious issue (Silveira & Perry, 1991; Livingstone & Hubel, 1988; Connolly & Van Essen, 1984; Malpeli *et al.*, 1993; Azzopardi & Cowey, 1995). Any such variation, however, would only be apparent behaviorally if the spatio-temporal properties of the stimulus allow M cells to determine luminance detection threshold and the P cells to determine colour thresholds.

Secondly, the relative loss in colour contrast sensitivity with eccentricity may be a consequence of unselective cone projections to the centre and surround of primate retinal P cells. Since early neurophysiological recordings were made from cone opponent neurons in the primate retina and LGN (De Valois *et al.*, 1958; Hubel & Wiesel, 1960; Wiesel & Hubel, 1966; Gouras, 1968) it was assumed that centre and surround of a receptive field are selective for cones of different types. Subsequently, it was suggested, largely supported by retinal anatomical data (Boycott *et al.*, 1987; Rohrenbeck *et al.*, 1989; Dacey *et al.*, 1996) that the projections of cones to retinal post-receptoral neurones may be unselective (Shapley & Perry, 1986). Under this scheme, termed the "hit and

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miss hypothesis", a ganglion cell receptive field will simply draw topographically from all the cones in that part of the retinal mosaic, and cone opponency arises from chance variations in the proportions of cone types projecting to the centre and surround regions of a receptive field. The idea of unselective cone projections finds some support from the neurophysiological literature (De Monasterio & Gouras, 1975; Kaplan *et al.*, 1989; Lennie *et al.*, 1991). These results suggest mixed cone surrounds but, as they have generally only been applied to P cells with a single cone centre, they have not addressed the selectivity of cone projections to multi-cone receptive field centres. In the primate fovea, midget P cells which have a single cone in the receptive field centre predominate, and further support for the unselective connections of cones is based on the criterion of sufficiency—that the addition of a mixed cone surround to a single cone centre is sufficient to account for the properties of foveal and parafoveal cone opponent neurons in the LGN (Lennie *et al.*, 1991), and the psychophysical colour-opponent channels (Paulus & Kroger-Paulus, 1983).

As a model of retinal connectivity, however, the "hit and miss" hypothesis is presently controversial (Rodieck, 1991; Shapley *et al.*, 1991; Reid & Shapley, 1992; Masland 1996). In particular, support for cone selectivity of centre and surround has emerged from direct measurements of primate retinal ganglion cell responses using a method of silent substitution (Shapley *et al.*, 1991; Reid & Shapley, 1992). These results support cone selective projections to centre and surround, even for centres with many cones. They are, however, presently based on a relatively small sample of neurons. Furthermore, they reveal much higher proportions of Type 2 neurons (cone selective with no spatial opponency) than have previously been reported (e.g., Derrington *et al.*, 1984; De Monasterio & Gouras, 1975). The issue of cone selectivity is presently an important one, revealing conflicting aspects of the physiological and anatomical results that remain to be resolved.

If cone opponency arises from chance variations in the proportions of cone types projecting to centre and surround regions of a retinal receptive field, clear predictions can be made about the loss of cone opponency which would occur as the average number of cones contributing to those receptive fields increases. It is known from both human and primate neurophysiological and anatomical data that there is an increase in average receptive field size with eccentricity in primate retina (Hubel & Wiesel, 1960; De Monasterio & Gouras, 1975; Shapley & Perry, 1986; Rodieck *et al.*, 1985; Watanabe & Rodieck, 1985). Although this is associated with a decrease in cone density with eccentricity, it can be calculated that there is still a net increase with eccentricity in the number of cones projecting to a receptive field.

Lastly, for the hit and miss hypothesis to be testable, one must ensure that an apparent loss in colour sensitivity is not a consequence of its method of measurement. For example, if a fixed spatial frequency is used to determine detection thresholds across the visual field, the relative increase in average receptive field size of the retinal neurons with eccentricity may produce an apparent loss in colour sensitivity. This effect occurs because individual P cells have different spatial passbands for colour and luminance contrast, such that colour sensitivity is lost relative to luminance sensitivity as spatial frequency increases (Derrington *et al.*, 1984; Ingling & Martinez-Uriegas, 1985). If a fixed spatial frequency is used to probe receptive fields of increasing size, a relative loss in colour contrast sensitivity will occur.

In this paper, we have developed a simple model calculating the loss of cone opponency across the visual field that would be expected assuming unselective cone projections, based on recent data for retinal P ganglion cell receptive field sizes in primate retina and cone densities from human retina. In order to compare this model to human psychophysical data, however, we have to eliminate the other potential sources of colour sensitivity loss described above. To avoid any contamination from a possible variation in the proportions of M and P cells in the retina, we have used stimuli modulated at a very low temporal rate (0.5 Hz). All our stimuli should thus be detected solely by the P cells pathways, as M pathways are extremely insensitive to luminance contrast at this spatio-temporal condition, and to colour contrast at all spatio-temporal conditions (Merigan, 1991). To avoid losses in colour sensitivity arising from the change in spatial scale with eccentricity, we have scaled our stimuli for each retinal location as described below. The results confirm that there is a selective loss of colour sensitivity over luminance sensitivity across the visual field, and show that a model of unselective cone projections is sufficient to account for the form of this loss for human vision.

THE MODEL

As the first step, we calculate how the preponderance of one cone type over another in a population will depend, on average, on the number of cones that are in that population. This is shown in Fig. 1(A). In this figure the short wavelength (S) cones have been ignored, and the only assumption we make is that the other two cone types, medium (M) and long (L) wavelength are present in the overall population from which they are drawn in the proportion of 2L:1M. The effect of this assumption is examined later. We calculate a measure of "average cone purity" for different sizes of cone population in the following way. For a population of N cones, each possible permutation of L and M cones is assigned a value representing its cone purity ranging from -1 to 1, where 0 represents equal numbers of cone types in a group and $+1$ or -1 indicates that all the cones are of one or the other type. The average cone purity is calculated from the sum of the products of each cone purity with its associated binomial probability. We discard the sign of

cone purity for this calculation so a value of unity represents both the all-L and all-M cone permutation.

Thus the average cone purity is given by:

$$\sum_{r=0}^{N} \left|\frac{N-2r}{N}\right| \frac{N!}{r!(N-r)!} p^r (1-p)^{N-r}$$

Where p = probability of L cone (0.67)
N = number of cones in group
r = number of L cones in each permutation and
$\frac{N-2r}{N}$ represents the cone purity value

A differential distribution of cone types in the centre and surround of a receptive field is required for a neuron to be cone opponent and thus colour sensitive. In Fig. 1(B) we show how the differential distribution of L and M cones to the centre and surround of a neuron's receptive field varies as the size of the cone population increases. We have thus defined a measure of "cone opponent purity" as being the difference in the cone purities of the centre and surround, which is re-scaled to range from 0 to 1. Thus the limiting value of 1 represents a unit with only L cones in the centre and only M cones in the surround or *vice versa*, whereas 0 indicates that there are the same proportions of L to M cones in both centre and surround of the receptive field.Thus the average cone opponent purity is given by:

$$\sum_{j=0}^{N_c} \sum_{k=0}^{N_s} 0.5 * \left|\frac{N_c - 2j}{N_c} - \frac{N_s - 2k}{N_s}\right| P_{c.j} P_{s.k}$$

Where p = probability of L cone (0.67)
N_c = number of cones in receptive field centre
N_s = number of cones in receptive field surround
j,k = number of L cones in each permutation of centre and surround, respectively
$P_{c.j}$ = binomial probability of cone permutation in centre and
$P_{s.k}$ = binomial probability of cone permutation in surround.

We have assumed a unit with a centre–surround arrangement with six times as many cones in the surround than the centre, and that the gains of the centre and surround are equal. Cone opponent purity applies to a particular unit, whereas the average cone opponent purity is applicable to a population of units all drawing on the same number of cones, and takes into account all possible combinations of all permutations of cones in both the centre and the surround of a unit. In Fig. 1(B) (lower panel) we show average cone opponent purity for two different ratios of cones in the overall population: 1L:1M and 2L:1M. The results show that this ratio makes very little difference to the variation in average cone opponent purity.

In order to apply this model to human psychophysical data, we need to know as accurately as possible the average number of cones projecting to cone ganglion cell receptive fields across the visual field. However, there are no direct primate data on the number of cones projecting to individual post-receptoral neurons across eccentricity,

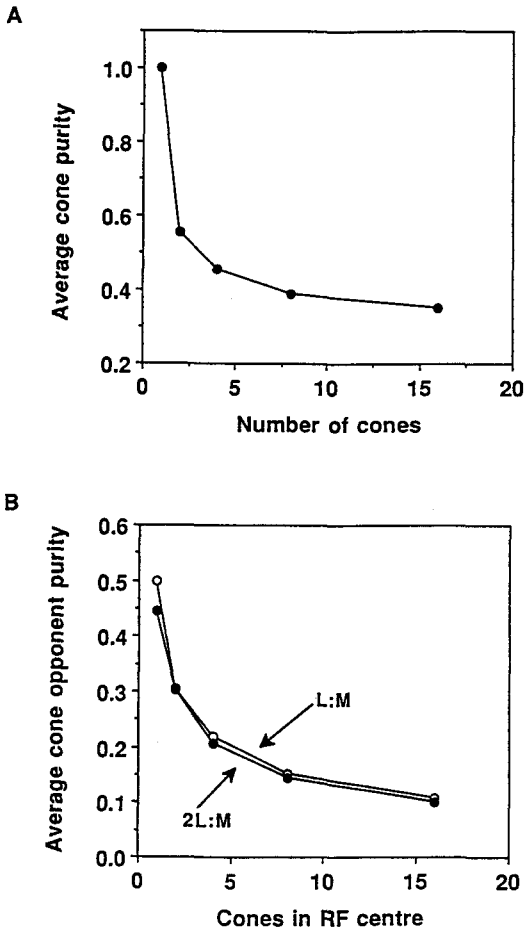

FIGURE 1. (A) The loss in average cone purity as a function of the number of cones in the group. This assumes cones in the ratio of 2L:M. (B) The loss in average cone opponent purity as a function of the number of cones in a receptive field centre. Calculated for a concentric centre–surround receptive field organization (type 1), and for two cone ratios of L:M and 2L:M as marked (see text for further details).

and this cannot be calculated from ratios of ganglion cell to cone densities, since each cone projects to a number of ganglion cells. To overcome this problem we have combined two different sources of data: neurophysiological data from macaque on retinal ganglion cell receptive field size, and anatomical measurements of cone densities in human retina. The data on receptive fields are from the results of Croner (1992) and Croner & Kaplan (1995), giving the centre size of macaque ganglion cells as a function of eccentricity. These data have the advantage that the P and M ganglion cells have been separately identified. We fitted a function describing receptive field area as a function of eccentricity based on the data of 55 retinal P-cells. Data giving the density of cones across the human visual field (Curcio *et al.*, 1990) were used to calculate the average number of cones per ganglion cell receptive field centre at different eccentricities. We used this function from 6 deg outwards, but extrapolated it back to the fovea assuming a receptive field centre size at the fovea of a single cone.

In Fig. 2 we combine the data for the number of cones per receptive field centre at different eccentricities with our model of average cone opponent purity. The figure

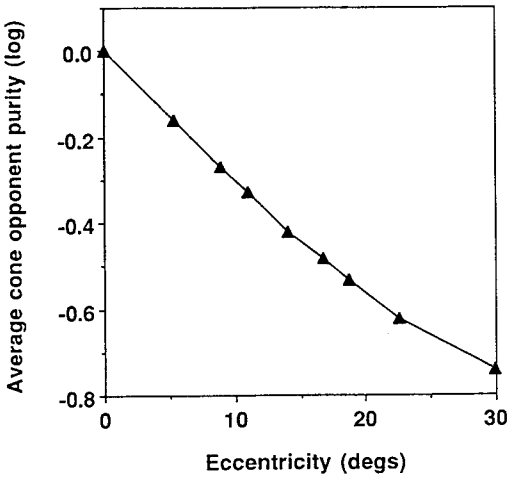

FIGURE 2. The model prediction of the loss in average cone opponent purity (log) as a function of eccentricity for human vision. The individual points arise from the calculated fit of the primate data for receptive field centre size multiplied by the human cone densities for that eccentricity. The cone ratio is 2L:M.

shows how, on average, cone opponency will be lost across the human visual field under the assumption of unselective cone connectivity. Thus the model predicts the relative decline in sensitivity between colour and luminance contrast, under the assumption that both colour and luminance contrast are detected by the P cell pathways. It is worth pointing out that the model is robust in not being critically dependent on the proportions of the two cone types in the overall population or on the number of cones in the receptive field surround. The model predictions are made without dependence on any critical free parameters.

COMPARISON WITH PSYCHOPHYSICAL DATA

The important prediction of the model is the form of the loss in colour contrast sensitivity relative to the loss in luminance contrast sensitivity across the human visual field. We have compared the decline in colour and luminance contrast sensitivities across eccentricity, using isoluminant red–green gratings and luminance gratings. Stimuli were generated using a VSG 2/1 waveform generator (Cambridge Research Systems) and displayed on a BARCO (CDCT 6551) RGB monitor. The CIE chromaticity coordinates of the monitor were $x = 0.60$, $y = 0.35$ for the red phosphor, and $x = 0.28$, $y = 0.60$ for the green phosphor. The output of the blue gun was set to zero. Data were collected on three subjects with normal colour vision (KTM, FAK, SR). Isoluminance was measured using a determination of perceived minimum motion; the subject adjusted the red–green mean luminance ratio of a grating (1 cpd, drifting at 1 Hz) to obtain a minimum in perceived velocity. An average of 10 settings was taken as the isoluminant ratio, which was measured at each eccentricity tested.

As raised in the Introduction, the selection of the stimulus parameters can influence the assessment of the relative colour and luminance contrast sensitivity loss.

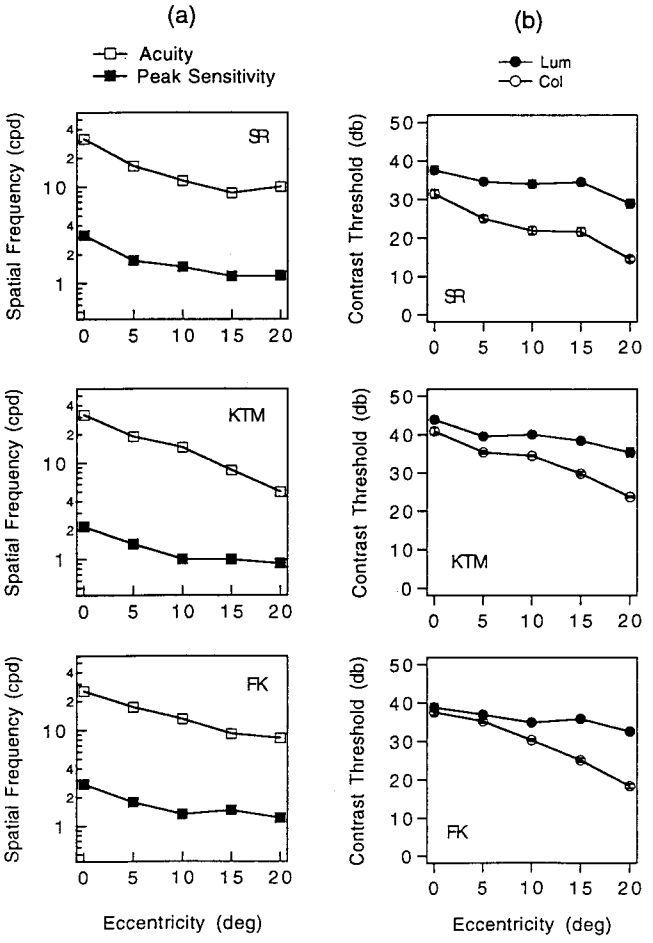

FIGURE 3. (a) The spatial frequency at the peak of the luminance contrast sensitivity function (solid symbols) and luminance contrast resolution (open symbols) as a function of eccentricity. (b) Luminance contrast sensitivity (solid symbols) and colour contrast sensitivity (open symbols) as a function of eccentricity. For each eccentricity, the spatial frequency of the luminance stumulus is that at the peak of the luminance CSF, and the spatial frequency for colour is 0.375 cpd (see text). Standard errors are equal to or less than the symbol size. Data for three subjects.

Firstly, we set the spatial extent of the stimuli so that the measured colour sensitivity was independent of any changes in spatial summation with eccentricity (Mullen, 1991). Stimuli were enveloped with a raised cosine envelope (λ = two spatial cycles) with a flat top of two spatial cycles. We confirmed that this stimulus size had no influence on the results by repeating the measurements (of Fig. 4) on one subject (FK) using an enlarged stimulus (a flat top of six spatial cycles in the same raised cosine envelope), which produced no change in the results. The temporal modulation used (0.5 Hz) produces optimal colour sensitivity at all eccentricities tested (Mullen, 1991). There is little change in the relative position of 0.5 Hz on the luminance temporal frequency contrast sensitivity function with eccentricity at this spatial frequency (Allen & Hess, 1992). We spatially scaled our stimuli for each retinal location so that chromatic and luminance contrast sensitivities were compared under optimum conditions, and at equivalent positions on their respective contrast sensitivity functions. To do this, we

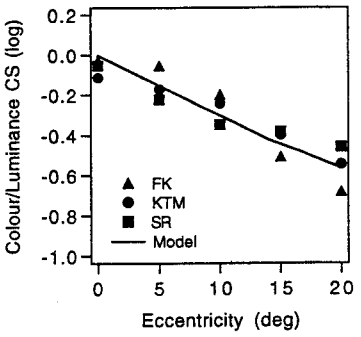

FIGURE 4. Data points show the ratio of colour to luminance contrast sensitivity for each subject. The line shows the model prediction from Fig. 2 fitted with a second-order polynomial. Data have been normalized (see text).

measured the colour and luminance contrast sensitivity functions at each eccentricity to be used in the experiment. At each retinal eccentricity, we determined the spatial frequency at the peak of the luminance contrast sensitivity function, and the spatial frequency at which maximum colour contrast sensitivity is obtained. Colour and luminance contrast sensitivities were then compared at these respective spatial frequencies at each eccentricity, ensuring that the comparison was made under conditions of optimum performance for each. The scaling eliminates an apparent loss in colour sensitivity that would be produced by sampling the colour and luminance pass bands at different relative positions at each eccentricity.

All measurements of contrast sensitivity were made using a method of adjustment, and were based on between four and five threshold settings for each spatial frequency. Complete contrast sensitivity functions were obtained, based on threshold measurements at seven spatial frequencies (0.25–16 cpd in one octave steps) for luminance detection and five spatial frequencies for colour detection (0.125–4 cpd in one octave steps), each at five retinal locations (0, 5 10, 15 and 20 deg). The luminance CSFs were fitted with a third-order polynomial function (on log–log coordinates) to determine the spatial frequency at the peak. The spatial frequencies at the peak luminance contrast sensitivity are plotted as a function of eccentricity in Fig. 3(a), and range between subjects from 2.2 to 3.2 cpd at the fovea to 0.9–1.2 cpd at 20 deg of eccentricity. These peak spatial frequencies were used for the comparison with colour contrast sensitivity. For the colour contrast sensitivity measurements, we selected a low spatial frequency (0.375 cpd) that gave optimum sensitivity at all eccentricities, since this spatial frequency lies within the lowpass region of our measurements of the colour CSFs at all eccentricities. Colour and luminance contrast sensitivities were then compared at their respective optimum spatial frequencies, over the same set of eccentricities, and are shown in Fig. 3(b).

The ratio of colour to luminance contrast sensitivity at each eccentricity is shown by the data points in Fig. 4 for the three subjects. The data have been normalized to the model by adjusting the vertical position of each subject's data set to as to minimize the mean absolute differences between the data and the model. This allows the relative slopes of the data and model to be compared. The results reveal a selective loss of colour contrast sensitivity, relative to luminance contrast sensitivity across the visual field. This is compatible with the selective loss of colour over luminance resolution across the visual field reported previously (Anderson *et al.*, 1991).

The model prediction is given by the solid line and shows that the assumption of random cone projections describes the form of the selective colour loss reasonably well. By contrast, the presence of cone-selective projections would require no selective loss of colour sensitivity to occur across the visual field. A measure of the goodness-of-fit of the model was obtained by calculating a χ^2 statistic for each subject's data, where $\chi^2 = \Sigma[(d_i - m_i)/\sigma_i]^2$. d_i and σ_i were the mean and standard deviations of the ith data point, and m_i its model prediction. Since the data represented the difference between colour and luminance contrast sensitivities, σ_i was calculated as $\sqrt{(\sigma^2_{i.\mathrm{col}} + \sigma^2_{i.\mathrm{lum}})}$ where $\sigma_{i.\mathrm{col}}$ and $\sigma_{i.\mathrm{lum}}$ were, respectively, the standard deviations of the individual colour and luminance contrast sensitivities. Each subject's data plot was vertically positioned to minimize the χ^2 statistic, thus fitting the model to the data with one free parameter. The resulting χ^2 values were FK = 6.51, KTM = 2.42 and SR = 1.92. With four degrees of freedom (five data points minus one free parameter) these χ^2 values are all smaller than the value of 9.49 needed to reject the model with 95% confidence. We conclude, therefore, that the selective loss in colour contrast sensitivity relative to luminance contrast sensitivity may be accounted for by the assumption of unselective post-receptoral cone projections in human vision. It is interesting to note that the model allows some colour opponency to be preserved even for quite high cone convergences: average cone opponency is approximately halved for an increase in cone convergence to the receptive field centre from 1 to 4, and approximately halved again for an increase to a 15 cone centre (Fig. 2). Furthermore, the non-selectivity of cone inputs need not arise in the earliest retinal stages (the connectivity of cones to horizontal and/or bipolar cells), but could occur later, for example in the connections of midget bipolar cells to ganglion cells which display a convergence in peripheral retina (Wassle *et al.*, 1994). As raised in the Introduction, the issue of cone selectivity is presently a controversial one. Although our model shows that the assumption of unselective cone projections is sufficient to account for the progressive loss of colour vision with retinal eccentricity, our methods do not allow this psychophysical result to be firmly attributed to particular anatomical levels or substrates. If, therefore, cone selectivity at the retinal level becomes firmly established, it suggests that colour information which is preserved in the parafoveal and peripheral retina by cone selectivity is lost at a higher stage of processing when the retinal

information is used to form the cortical colour and luminance mechanisms.

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Acknowledgements—We thank Lisa Croner and Ehud Kaplan for supplying us with their primate data prior to publication. We thank Marty Banks for helpful discussion in the early stages of the study, and Gordon Legge for helpful comments. We thank Stephane Rainville for his work as a subject. The work was supported by grants from the Wellcome Trust of Great Britain and the Medical Research Council of Canada (grant numbers MT-10819 and MT-11554).