

Perceived shifts in saturation and hue of chromatic stimuli in the near peripheral retina

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Using an asymmetric color matching technique, we measured the perceived changes that occur in the saturation and hue of colored stimuli at different eccentricities within the central 25° of the human retina in nine color-normal subjects. A cone-opponent-based vector model was used to compute the activity of the $L-M$ and $S-(L+M)$ channels. The results show that a large proportion of the shifts in saturation and hue that occur with increasing retinal eccentricity are mirrored by decreased activity of the $L-M$ channel. In comparison, the contribution of the S cone-opponent system undergoes relatively little change within the central 20°. In addition, we also found that changes in saturation and hue are different from each other in terms of their variation across color space and their variation with stimulus size. Our findings suggest that perceived shifts in saturation and hue are mediated largely via the reduction in activation of the $L-M$ cone-opponent channel but that saturation and hue might be subject to different retinal and/or cortical influences that contribute to their differing size dependencies in the peripheral retina. © 2007 Optical Society of America

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1. INTRODUCTION

When colored stimuli move from central to more peripheral regions of the retina, human observers often report changes in their appearance that can be expressed in terms of shifts in their perceived hue and saturation [1–10]. The observed changes in hue that occur with increasing retinal eccentricity vary in magnitude and are dependent upon factors such as the original hue of the stimulus [5,6,9,10]. Changes in saturation typically lead to colored stimuli being perceived as more desaturated or “washed out” as they move to the retinal periphery [2–4,7,11–14].

The cause of these perceived changes in the quality of color vision in the retinal periphery has been attributed to a number of different factors. Early ideas suggested that altered color perception in the retinal periphery represents a zonal reorganization of chromatic processing, with the central retina mediating trichromatic, the midperiphery dichromatic, and the far periphery monochromatic color perception [11,15–18]. Other explanations have concentrated on the possibility that rods, which have a greater predominance in the peripheral retina, can somehow influence or alter the chromatic signal in the retina. A number of studies have demonstrated that rod influence can generate a variety of complex effects on both the hue and saturation of colored stimuli in the retinal periphery [3–5,19–30]. Poorer sampling of the retinal image by cone photoreceptors in the retinal periphery has also been implicated in the degradation of color perception. Long-wavelength- (L -) and middle-wavelength- (M -) sensitive cone densities are known to steadily decrease with increasing retinal eccentricity, whereas short-

wavelength-sensitive- (S -) cone density remains relatively constant outside the central 7° [31,32]. However, a number of studies have shown that the effects of poorer L - and M cone sampling can be negated, and normal color sensitivity and appearance effectively restored, if peripherally presented stimuli are sufficiently large [12–14]. Thus color vision might be thought of as being size scaled across the retina, with increases in stimulus size compensating for increases in spatial summation areas for chromatic mechanisms [6,33–35]. The concept of a “perceptive field,” introduced by Abramov and colleagues, embodies this idea [12].

Recent behavioral studies have raised the possibility that the reduction in the quality of color perception in the retinal periphery is the result of differential losses in sensitivity between the $L-M$ and $S-(L+M)$ cone-opponent mechanisms [34–37]. They show that $L-M$ cone-opponent function is best developed in the central visual field but becomes increasingly more degraded in the retinal periphery. The $S-(L+M)$ system, on the other hand, is comparatively more resistant to the constraints placed on chromatic processing in the peripheral retina with its function changing to a lesser degree with increasing eccentricity [36–39]. However, while these studies agree that the relative efficiencies of the two cone-opponent mechanisms vary from central to peripheral retina, the underlying reasons for these changes remain contentious. On the one hand, differences between the operation of the $L-M$ and $S-(L+M)$ mechanisms in the retinal periphery are attributed to the loss of cone-selective connectivity to the midganglion cells (substrate of the $L-M$ system), which exists in the fovea but becomes increasingly more

random in the periphery [36,40,41]. On the other hand, there are those studies that suggest that cone-selective connectivity is maintained in the peripheral retina and that any reduction in performance between the cone-opponent mechanisms is imposed by central cortical mechanisms [38,42,43].

Regardless of the differing viewpoints as to the underlying nature of the differential functional loss between the $L-M$ and $S-(L+M)$ cone-opponent mechanisms, it is pertinent to establish the role of cone opponency in producing the phenomena we describe. This study focuses on the extent to which observed saturation and hue shifts for chromatic stimuli can be accounted for by the changing pattern of dominance between the two cone-opponent systems that occurs with increasing retinal eccentricity. This paper represents an extension of our previously published work in which we examined the relationship between perceived changes in hue with retinal eccentricity and their relation to unique hues [10,39]. We employed an asymmetric matching paradigm to measure shifts in perceived saturation and hue that occur between peripherally presented colored test stimuli and centrally located reference stimuli [2]. In the present study we modeled the results using a simple cone-opponent vector model. This model is based upon original ideas by Ingling and Tsou [44], subsequently modified by Stanikunas and colleagues [45]. It allows us to compare the magnitudes of activation generated in the cone-opponent mechanisms by centrally presented chromatic stimuli with those generated by matched test stimuli that are presented in the retinal periphery. Cone-opponent activation is computed on the basis of linear summing and differencing interactions between L , M , and S cones along lines similar to those that operate in retinal ganglion cells [46,47].

We were also interested in the extent to which perceived changes in saturation might be dissociable from those that occur in hue with increasing retinal eccentricity. Perceived shifts in hue and saturation have been shown to occur in tandem with each other [2] to the extent that certain studies have raised the possibility that they are interlinked [27]. However, recent studies suggest that, on the basis of differences in perceptive field sizes, different physiological mechanisms might contribute to hue and saturation changes [48]. In an attempt to reconcile these differing viewpoints, we measured how perceived hue and saturation changes varied as a function of location of the stimulus in color space and as a function of stimulus size.

2. METHODS

A. Stimuli

Circular test-and-probe stimuli were generated on a high-resolution graphics monitor (Sony GDM520) using purpose-built software to drive a VSG 2/5 video graphics card (Cambridge Research Systems Ltd., Rochester, United Kingdom). Stimulus chromaticity was defined as a vector in CIE color space taking 0° , as defined in MBDKL space, as the starting point. Departures from this are defined as angular rotations in CIE color space (chromatic axis, ϕ). The 0° – 180° and 90° – 270° directions depict the $L-M$ and $S-(L+M)$ cardinal axes in both color spaces

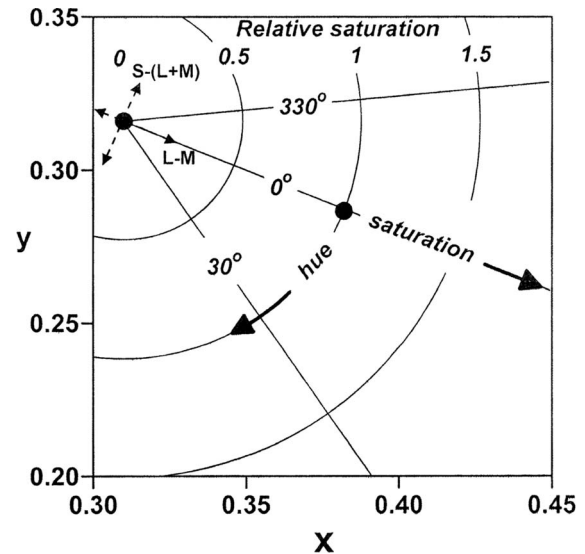


Fig. 1. Section of the CIE (1931) chromaticity diagram showing the direction of changes that occur across color space when hue and saturation are altered. The concentric circles indicate the nominal vector length of unity together with higher and lower values (1.5 and 0.5). The black circles depict the background chromaticity ($x=0.31$, $y=0.316$) and the 0° (cardinal red) stimulus ($x=0.382$, $y=0.287$). To match saturation, the stimulus was changed by moving along the 0° vector. To match hue, the stimulus was rotated in color space while keeping the vector length constant. The location of the cardinal $L-M$ and $S-(L+M)$ cone-opponent axes are also indicated. Note that all probe stimuli were presented with a vector length of 0.5.

(see Fig. 1). Note that a distinction should be drawn between the physical manipulations described in terms of the colour space used and the perceptual variations that we have measured. Observers used the perceptually based attributes of hue, saturation, and brightness to match color samples, manipulating the physical characteristics of chromatic axis, purity, and luminance. In this study our term hue shift refers to the rotation of chromatic axis (in degrees) in CIE 1931 color space needed in order for the peripheral test stimulus to match the parafoveal probe. Similarly, our term saturation ratio refers to changes in purity that are required to produce matches. Physically, the stimulus was manipulated by adjusting the length (i.e., purity) and orientation (i.e., chromatic axis) of a straight vector from the background (CIE $x, y, =0.31, 0.316, Y=12.5 \text{ cd m}^{-2}$; see Fig. 1). Stimuli of equal vector length formed a circle in CIE (1931) color space. Saturation ratio values equal to unity indicated that no perceived shift in saturation occurred and required no change in vector length. Ratios >1 indicated that the peripheral test stimulus had to be increased in purity in order to counteract the perceived desaturation that has occurred and vice versa. One consequence of using these physical manipulations is that equal magnitudes of shift do not have the same perceptual meaning in different areas of color space. For a fuller description of the methods and calibration procedures see Parry *et al.* [10]

B. Psychophysical Procedure

In order to measure the perceived changes in saturation and hue that take place when stimuli are shifted to eccen-

tric retinal locations, we employed an asymmetric matching paradigm. In this task, a 1 deg diameter probe stimulus was presented at a nasal eccentricity of 1 deg for a period of 380 ms. Simultaneously, a test stimulus was presented at a greater eccentricity. The observers' task was to change the eccentric test stimulus so that it matched the parafoveal probe in terms of saturation, hue, and brightness. Viewing distance was always 50 cm, and a small black fixation mark was provided. Viewing was monocular, and a mild head restraint was provided. The experiments were carried out in a dimly lit room after at least 10 min adaptation to the background chromaticity.

Method of adjustment was employed to generate matches between eccentric test and parafoveal probe stimuli, the subject having free control over the chromatic axis, purity, and luminance of the test stimulus. Vector length was 0.5, and luminance was 12.5 cd m^{-2} . After a pair of stimuli was presented, the subject adjusted one of the three test parameters, rotating the chromatic axis in steps of 5 deg, changing vector length in steps of 0.1 or changing luminance in steps of 0.01 cd m^{-2} . Therefore there were six possible responses, for which the subject was provided with three up-down levers (CB3 response box, Cambridge Research Systems Ltd., Rochester, United Kingdom). After a single adjustment, there was an additional 500 ms interval before the new pair was presented, which meant that the stimuli were presented approximately every 2 to 3 s, depending upon the observers' decision time. Once the subject was satisfied that the two stimuli were matched for all three parameters, they pressed a key that advanced the hue of the probe stimulus by $\phi=15^\circ$. The matching procedure was then repeated. Initially, the three physical settings were unchanged from the previous match. The experiment was concluded when 25 probe chromatic axes had been tested, from $\phi=0^\circ$ to 360° in 15° steps; 0° and 360° stimuli were repeated presentations of the same color at the start and at the end, respectively, of an experimental run. This was done in order to assess the extent of differences in matching that might have been due to any change in adaptational state. There was no systematic difference between these repeated values. In additional control experiments we varied the order of the chromatic stimuli using steps of $\phi=105^\circ$ so that adjacent stimuli in color space were never assessed in adjacent trials. In these control experiments at the beginning of each trial we also reset the hue and saturation of the central reference and peripheral test stimulus so that they were identical at the beginning of each trial. These changes in ordering had no effect on the observed pattern of effects obtained with the sequential ordering.

C. Subjects

Nine color-normal subjects participated in this study. All subjects compared parafoveal probe and peripheral test stimuli at nasal eccentricities of 1 and 18 deg, respectively. There were four males and five females, all of whom had normal color vision and best corrected acuity of 6/6 or better. Mean (± 1 s.d., s.d., standard deviation) age was 33.8 (9.6). Three of the male subjects were the authors. The other six subjects were naive as to the precise nature of the investigation, but all were well-practiced

psychophysicists. All subjects gave informed consent to the experiments, which were carried out in accordance with the Declaration of Helsinki.

D. Cone-Opponent Vector Model

In order to examine the properties of peripheral color vision in terms of a cone-opponent model, we have used the photoreceptor-to-mechanism transformation described by Stanikunas *et al.* [45] and by Murray *et al.* [39]. The model was developed using Smith-Pokorny fundamentals [49]. This model, like the majority of cone-opponent models, is linear because most visual mechanisms respond linearly, at least for threshold and close-to-threshold perturbations. Nonlinearities are largely ignored (see [50]), an approach that is justified by the fact that the models account for many observations such as spectral sensitivity and wavelength and saturation discrimination [44,51]. Cone-opponent activation of the $L-M$, $S-(L+M)$, and achromatic $L+M$ mechanisms are computed from Eq. (1):

$$\begin{bmatrix} L+M \\ L-M \\ S-(L+M) \end{bmatrix} = \begin{bmatrix} 0.63 & 0.395 & 0 \\ 2.21 & -2.6 & 0 \\ 0.35 & 0.35 & -1.02 \end{bmatrix} \begin{bmatrix} L \\ M \\ S \end{bmatrix}. \quad (1)$$

Figure 2 illustrates the functions obtained for all of the probe stimuli based upon Eq. (1). The cone fundamentals were normalized to illuminant C, as this was the background chromaticity. In addition to so-called small signal linearity, the following assumptions apply: (i) Opponent functions are zero for illuminant C. (ii) Opponent functions are assumed to be orthogonal to each other; that is, the $L-M$ function should have zero response at violet and cardinal yellow and the $S-(L+M)$ function should have zero response at cardinal red and green [52]. (iii) Luminance is based on a ratio of 1.6 between L and M , although it is well known that in the population the actual ratio of L and M cones varies over a wide range [53]. Varying this ratio affects only the luminance channel. Note that this model is concerned primarily with the second stage of cone opponency. As such, it neither attempts to account for the differences between threshold and suprathreshold observations, nor does it deal with the fact that, perceptually, there is almost certainly an S cone input to the perception of redness [54]. According to Ingling

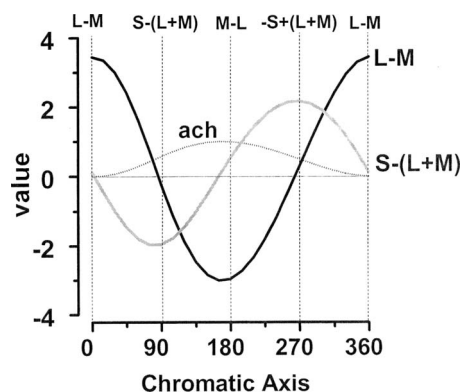


Fig. 2. Magnitude of activation generated by the probe stimuli in the $L-M$ and $S-(L+M)$ cone-opponent as well as the $(L+M)$ nonopponent (luminance) mechanisms. The values of activation were calculated using Eq. (1) (see methods).

and Tsou [44], this occurs at a subsequent stage of color processing. There is therefore no *S* cone opponent input to the *L-M* component in Eq. (1).

3. RESULTS

A. Perceived Saturation as a Function of Chromatic Axis

In this series of experiments we wished to investigate whether perceived changes in hue and saturation fol-

lowed similar patterns for stimuli from different regions in color space. Figure 3(a) shows the group averaged results ($n=9$) for perceived saturation and hue shifts, and Fig. 3(b) the individual saturation data for a test stimulus of 3° diameter at a retinal eccentricity of 18° as a function of parafoveal probe chromatic axis. The changes in perceived hue (solid gray curve) are described in detail elsewhere along with the individual data [10]. Summarizing these perceived changes, the variation in hue with increasing retinal eccentricity is not uniform across color

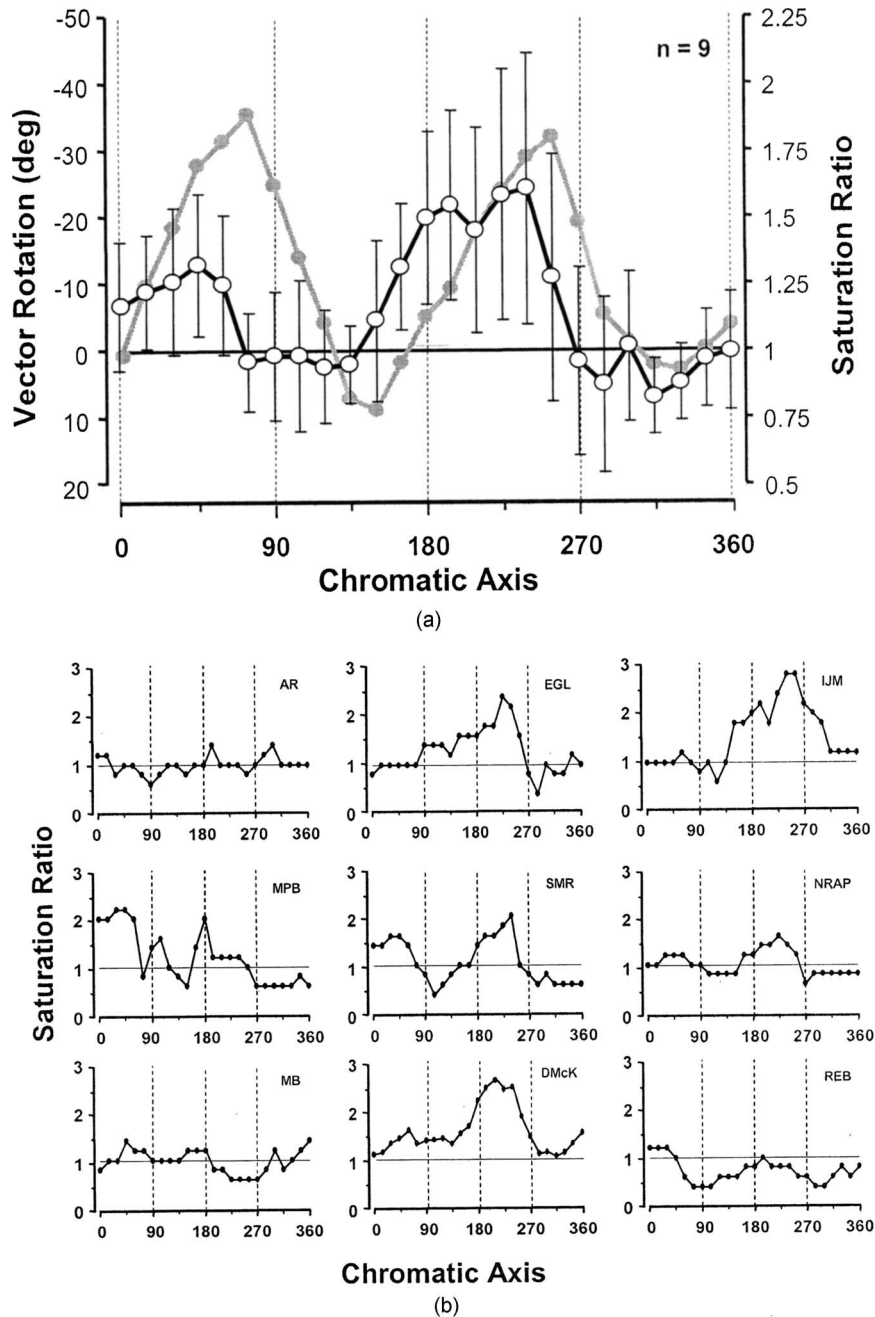


Fig. 3. (a) Group-averaged results for perceived hue and saturation shifts measured as a function of probe chromaticity. The data were obtained for a 3° diameter stimulus at an eccentricity of 18° . Saturation changes (black curve) are expressed in terms of saturation ratio (see methods) as indicated on the right-hand *y* axis. Error bars depict +1 S.D. of the mean. Hue changes (gray curve) are measured in terms of the magnitude of rotation (degrees) in color space necessary for the peripheral test stimulus to match the central probe, as shown on the left-hand *y* axis. (b) Individual data from all nine subjects upon which the average in (a) is based.

space, with certain hues experiencing large perceived shifts, while others remain largely invariant. In essence, the shifts in hue that occur with increasing retinal eccentricity can be simply characterized as being either toward blue or yellow. In the pink/purple region of color space ($\phi=0^\circ-130^\circ$) a negative rotation of the test stimulus hue vector is required in order to counteract its perceived (positive rotational) shift toward blue and make a match with the more centrally located test stimulus. Similarly, in the cyan region ($\phi=135^\circ-170^\circ$) the tendency of the peripheral test to appear more bluish has to be counteracted by a positive hue rotation in order to make a match. Beyond $\phi=180^\circ$ the perceived hue shifts are toward yellow, so negative rotational shifts of the test stimulus are required to counteract this tendency between $\phi=180^\circ-290^\circ$ and positive shifts are required between $\phi=290^\circ-360^\circ$.

As has been reported previously [2], the tendency is for colors to appear more desaturated in the retinal periphery. Like the shifts in hue, the perceived saturation shifts [solid black curve in Fig. 3(a)] are nonuniform across color space. However, it is apparent that the two functions are not in phase. The averaged data indicate that the largest saturation ratios (i.e., those colors that appear most desaturated) occur for stimuli in the green region of color space ($\phi=210^\circ-250^\circ$), and there is a smaller localized maximum in the nonspectral pink region of color space ($\phi=0^\circ-50^\circ$). Stimuli in two regions of color space, $\phi=70^\circ-135^\circ$ (violet and cyan) and $\phi=270^\circ-320^\circ$ (yellow

and orange), exhibit smaller changes in perceived saturation. However, it should be noted that the changes in perceived saturation exhibit a large degree of intersubject variability, greater than that shown for perceived hue shifts [10], with three of the subjects (AR, MB, and REB) showing little or no perceived shift in saturation.

Figure 4 shows levels of activation generated in the $L-M$ and $S-(L+M)$ cone-opponent mechanisms by the peripherally matched stimuli and the parafoveal probe stimuli for all nine observers. The data are based upon calculations from Eq. (1). Note that only the two cone-opponent mechanisms are illustrated here and in subsequent figures. Observers were able to find a satisfactory match without changing luminance. Again, note that increases in the magnitude of opponent activation are due to the compensatory adjustments that have to be made by the subjects in order for the peripheral stimuli to match the parafoveal probes. Therefore, increases in the amplitude of the functions denote decreases in activation caused by the saturation shifts that occur in the peripheral test stimuli, and vice versa. Figures 4(a) and 4(b) plot the group-averaged data for $L-M$ and $S-(L+M)$ activation. While there is a large degree of intersubject variability [see Fig. 3(b)], the group-averaged data highlight certain trends. In particular, the perceived changes in saturation that occur in the retinal periphery appear to be mirrored by greater changes in the level of activation of the $L-M$ compared with the $S-(L+M)$ cone-opponent system. The difference between the levels of activation for

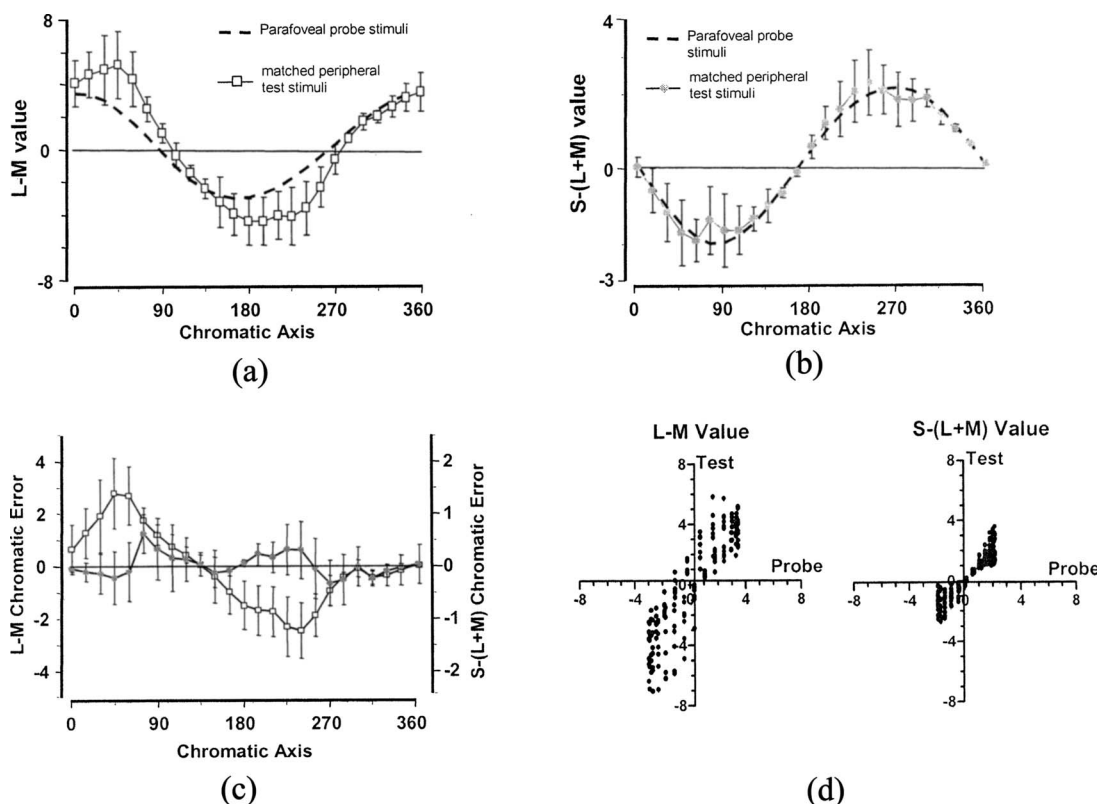


Fig. 4. Group-averaged data showing the levels of activation generated in the $L-M$ (a) and $S-(L+M)$ (b) cone-opponent systems generated by peripherally matched test stimuli compared with the central probe stimuli. (c) Difference plots of the data in (a) and (b) for the $L-M$ and $S-(L+M)$ cone-opponent systems. Error bars depict 95% confidence intervals. (d) Scatter plots showing the correlation between test and probe for $L-M$ and $S-(L+M)$. Individual data points represent the value obtained for the peripheral test target plotted against the value for the 1° probe for all viewing conditions and all subjects.

the matched test stimuli and the probe stimuli in the two cone-opponent systems, defined as chromatic error, is illustrated in Fig. 4(c). Chromatic error was calculated as

$$e_{\phi} = V_{\text{test}} - V_{\text{probe}}, \quad (2)$$

where e_{ϕ} is chromatic error for each chromatic axis and V_{test} and V_{probe} are the activation values for test and probe, respectively.

Figure 4(d) illustrates scatter plots of test versus probe for all subjects comparing the $L-M$ value (left panel) with the $S-(L+M)$ one (right panel). If chromatic error was zero and the eccentric test matched the parafoveal probe exactly, then all the data in Fig. 4(d) would lie on a straight line. It is clear that the degree of association between test and probe is greater for the $S-(L+M)$ mechanism than for the $L-M$ mechanism. To quantify this, we calculated RMS chromatic error for each axis, defined as

$$\sqrt{\frac{\sum e^2}{n}}, \quad (3)$$

where e =chromatic error and n is the number of subjects. The $L-M$ error=1.6 and the $S-(L+M)$ error=0.5. Evidently, it is changes in the output of the $L-M$ opponent system rather than the $S-(L+M)$ system that account for the perceived color changes that occur in the near peripheral field. Hue shifts are manifest as a change in phase of the functions, which is more evident in $L-M$ than in the $S-(L+M)$ cone-opponent activation.

B. Perceived Saturation and Stimulus Size

It has been suggested that the quality and nature of color perception experienced in the peripheral retina is strongly dependent upon the size of the chromatic stimulus [12]. To investigate this further, we conducted more intensive experiments on two observers (both authors). In this experiment we were interested in how the saturation and hue match across different axes in color space reflected this dependency. Figures 5(a) and 5(b) illustrate data from two observers for 18° eccentricity. In the first column the variation in perceived hue (gray symbols, left-hand axis), and saturation (black symbols, right-hand axis) are plotted for different chromatic directions in color space. Test stimulus diameter is indicated on the right-hand side of the figure. In line with our earlier report [10], the perceived shifts in hue appear to be relatively immune to changes in stimulus size. Even for the largest stimulus sizes, significant rotations in chromatic axis are required in order for the peripheral test stimuli to match the central probe stimuli in terms of their hue. All sizes produce prominent peaks in the hue matching function in the pink/purple ($\phi=30^{\circ}-70^{\circ}$) and green/yellow ($\phi=220^{\circ}-260^{\circ}$) regions of color space. These changes in hue are in marked contrast to the changes in perceived saturation, which although readily apparent for the smallest stimulus sizes, are greatly reduced with increasing stimulus size.

The second column illustrates the same data in CIE 1931 color space. The gray circles depict the chromaticities of the parafoveal probe, and the joined black symbols the peripherally matched chromaticities. These plots mask the shifts in hue but readily depict the direction of

the perceived saturation shift in color space. It is apparent from both the shifts in saturation in column 1 and the distortion of the color circle in column 2 that the perceived changes in saturation are dependent upon stimulus size. For small stimulus sizes ($<4^{\circ}$) there are large desaturation effects for stimuli that lie in the cyan/green region of color space ($\phi=200^{\circ}-250^{\circ}$) and to a lesser extent for those that lie in pink regions ($\phi=20^{\circ}-50^{\circ}$). As the peripheral test stimulus increases in size, the saturation ratios fall to one and in some cases below one. In this case the x and y chromaticities of the eccentric test stimuli appear inside the color circle for the parafoveal probe stimuli. This effect of saturation increase is particularly evident for subject NRAP.

The third and fourth columns of Fig. 5 show how the perceived saturation shifts for different stimulus sizes affect the activation in the $L-M$ and $S-(L+M)$ cone-opponent mechanisms. When expressed in these terms, peripheral desaturation for small stimuli is much larger in the $L-M$ system than the $S-(L+M)$ system. As stimulus size increases, the perceived changes in saturation are abolished and the level of activation in the $L-M$ opponent system by the eccentric test stimuli approaches that produced by the parafoveal probes.

C. Perceived Saturation and Retinal Eccentricity

In order to investigate the effects of increasing eccentricity in more detail, the three authors participated in further experiments. Figure 6 shows data obtained with a peripheral test stimulus 3° in size, presented at retinal eccentricities (as indicated on the right-hand side of the figure) of 12°, 18°, and 24° for subject DMcK [Fig. 6(a)] and 6°, 12°, 18°, and 24° for subjects NRAP [Fig. 6(b)] and IJM [Fig. 6(c)]. The columns of data are the same as for Fig. 5. The data echo the effects shown for stimulus size, the output of the $L-M$ system appearing to be more vulnerable than the $S-(L+M)$ system as retinal eccentricity increases. At the lowest eccentricities, saturation shifts are minimal and hence there is little difference in the magnitude of opponent activation produced by the peripheral test stimuli compared with the central probes. With increasing retinal eccentricity, the saturation shifts are represented as a compensatory increase in the output of the $L-M$ system with the $S-(L+M)$ system being relatively unaffected. Beyond 20°, large changes in the output of the $L-M$ system are accompanied by decreases in activation of the S cone-driven system, which presumably would become even more manifest at larger eccentricities [37].

4. DISCUSSION

A. Relative Strength of $L-M$ and $S-(L+M)$ Cone Opponency in the Peripheral Retina

In this study we have employed a matching paradigm to assess separately the changes that occur in perceived hue and saturation of colored stimuli in the retinal periphery. Our modeling of cone-opponent functions based on this matching data reveals that the perceptual shifts observed are mirrored by a reduction in the activation of the $L-M$ opponent system. By comparison, the S cone system remains relatively stable in terms of its output within

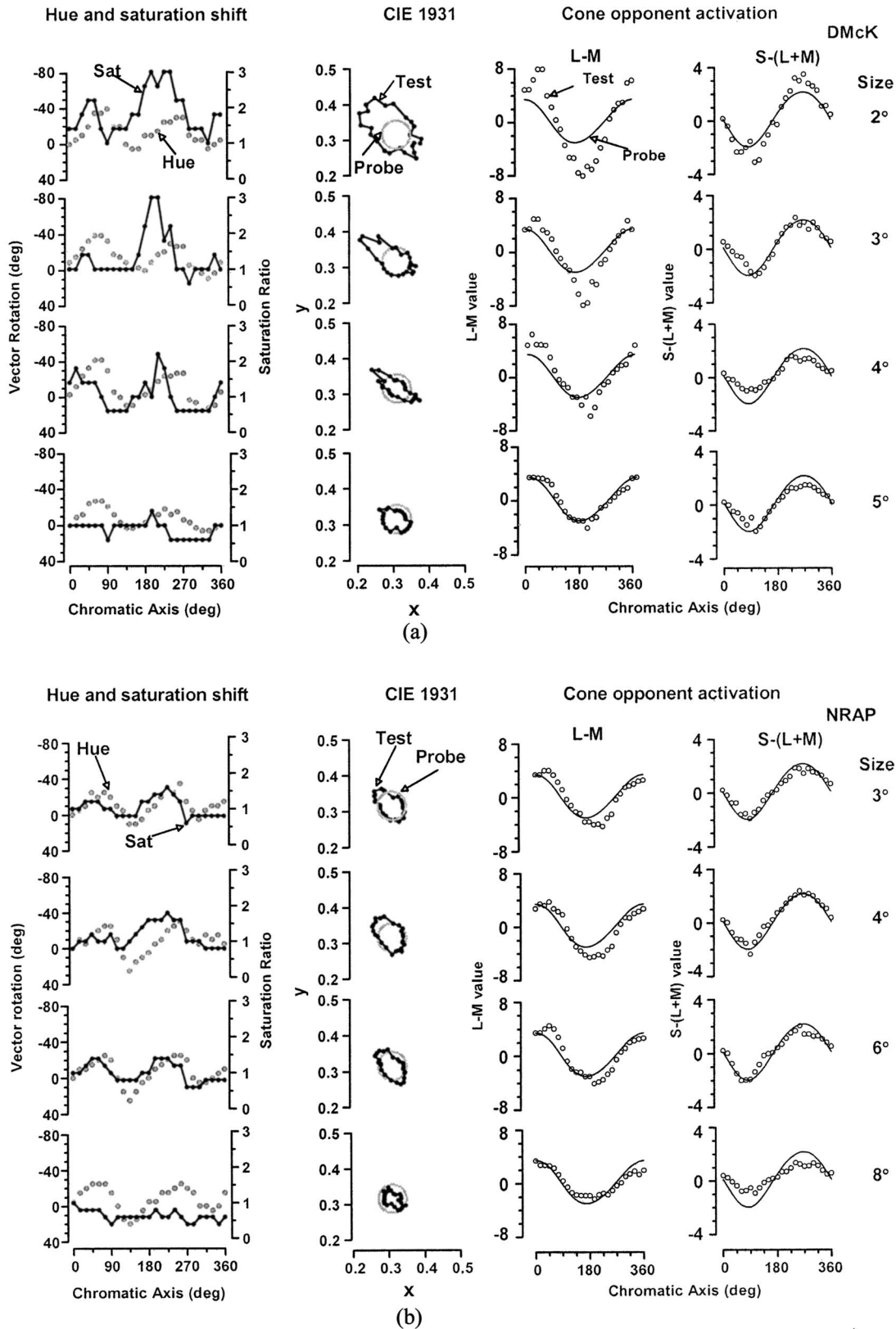


Fig. 5. Saturation and hue shifts as a function of test stimulus size. The first column plots the hue and saturation shifts for a particular stimulus size as a function of probe chromatic axis. The second column plots the locus of the central probe (gray circle) and the matched peripheral test stimuli (black curves) in terms of their 1931 CIE chromaticity coordinates. The last two columns plot the activations produced by the peripherally matched test stimuli in the $L-M$ and $S-(L+M)$ cone-opponent mechanisms calculated using Eq. (1). Data shown are for two subjects, DMcK (a) and NRAP (b), for test stimuli at a constant retinal (nasal) eccentricity of 18° .

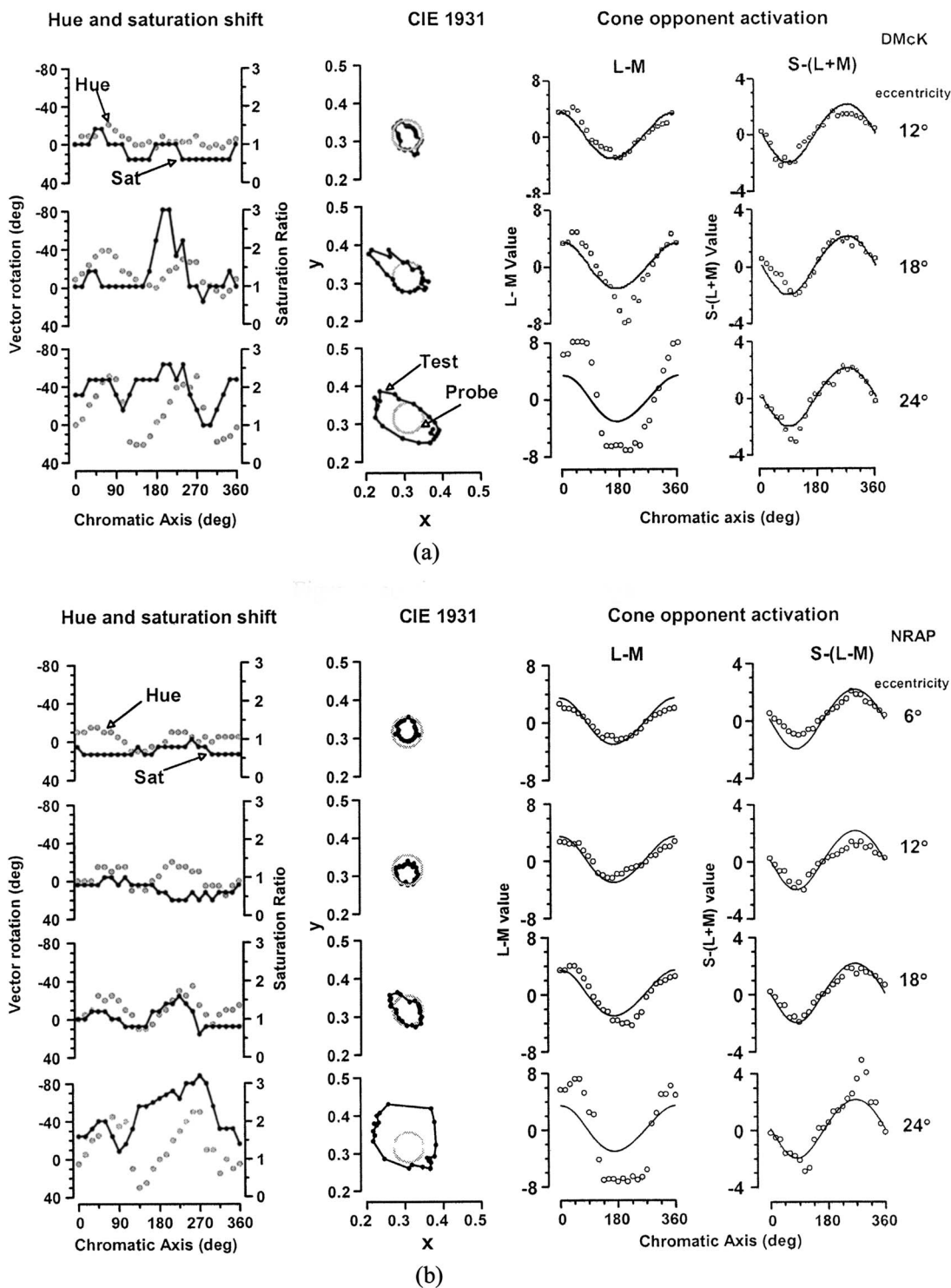


Fig. 6. Caption appears on following page.

the central 18° of the retina. It seems that the *S* cone-opponent system becomes more predominant in the retinal periphery, while the *L-M* system is more important in central rather than peripheral vision.

The differential loss in function between the *L-M* and *S* cone-opponent systems may have a number of possible causes. The changing pattern of dominance might be attributable in some part to the changes in cone photoreceptor density that occur with increasing eccentricity. *L* and

M cone density is greatest in the central fovea, and falls steadily with increasing retinal eccentricity. *S* cone density, on the other hand, while being zero in the central fovea, increases to a maximum at about 2°, then falls with increasing eccentricity up to 7°–10°, beyond which it remains relatively constant [31,32]. Another reason might be the changing nature of cone inputs to the opponent mechanisms with retinal eccentricity. Physiological and behavioral evidence suggests that while cone-selective

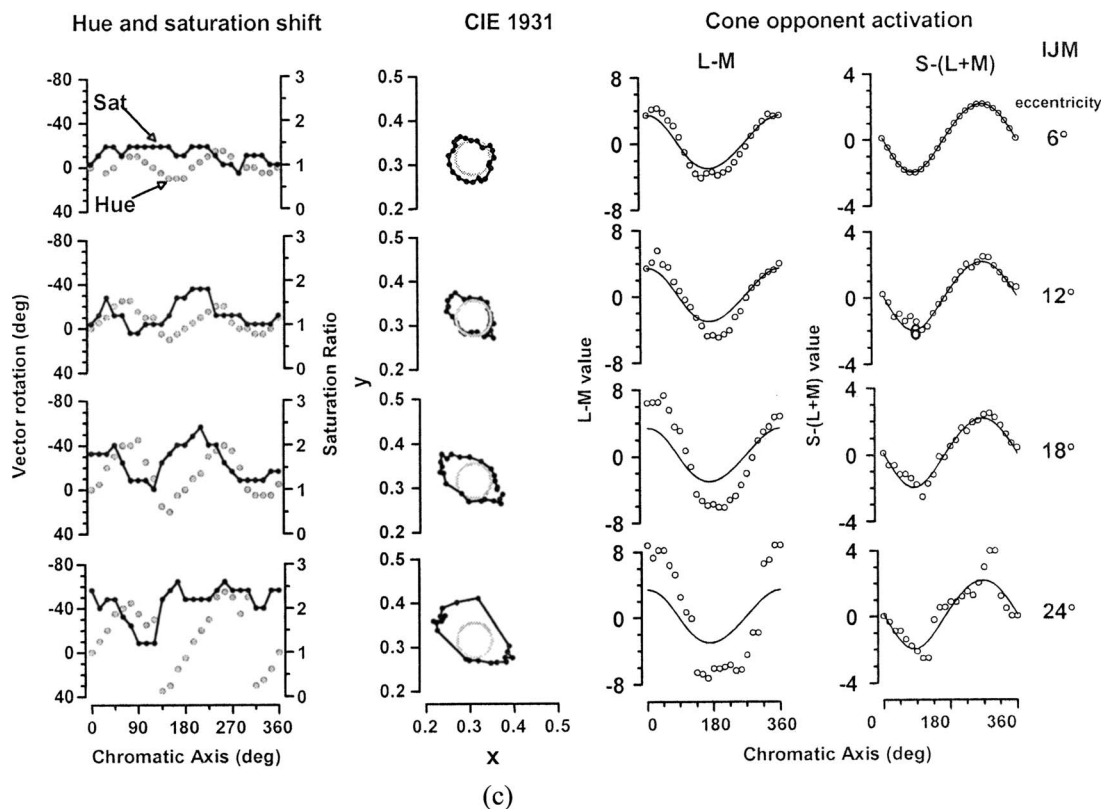


Fig. 6. Saturation and hue shifts as a function of retinal eccentricity. Data are presented in the same format as for Fig. 5 and show the hue and saturation shifts, the location of probe and matched test stimuli in CIE space, and the $L-M$ and $S-(L+M)$ cone-opponent activations generated for peripheral test stimuli of increasing eccentricity and constant diameter (3°). Data shown are for three subjects, DMcK (a), NRAP (b), and IJM (c).

connectivity with small bistratified ganglion cells may be a consistent unvarying feature of the S cone-opponent pathway with increasing retinal eccentricity, the nature of cone connectivity with the midget ganglion cells of the $L-M$ system becomes less clear cut [36,43,47,55–57]. $L-M$ opponency is maintained in the central retina by antagonist single cone input to the centre and surrounds of the midget ganglion cell receptive field [58,59]. Certain studies indicate that this cone-selective input is reduced in the retinal periphery, where multiple cone inputs to the centers, and possibly the surrounds, of receptive fields take on a more random pattern of connectivity [60,61]. The emergence of this nonselective or random cone connectivity has been proposed as a reason for the reduction in chromatic sensitivity that has been measured in psychophysical studies for the $L-M$ system [36]. This hypothesis is consistent with some *in vitro* studies. For example, Diller *et al.* [38] compared L and M cone inputs to peripheral ganglion cells and found virtually all of the midget ganglion cells sampled to be nonopponent. However, other studies contradict this view. Martin and co-workers have demonstrated that a high proportion (>80%) of midget ganglion cells have strong cone opponency and high chromatic sensitivity [42,62]. The idea that $L-M$ opponency is preserved in the peripheral retina also gains support from other behavioral studies that show that as long as stimuli are suitably scaled in size, then chromatic sensitivity is preserved [38]. These studies continue to emphasise the fact that the $L-M$ opponent system is specialized for central vision, with $S-(L+M)$

opponency becoming increasingly more important in the periphery. However, they consider these differential effects to be the result of inequalities in the cortical magnification factors for the $L-M$ and S cone-driven opponent systems, rather than fundamental changes in the connectivity of cones with the opponent midget ganglion cells [38]. The results from the present study do not resolve the debate as to whether changes in $L-M$ cone opponency are due to centrally based cortical mechanisms or due to changes in cone connectivity in the retina—they do, however, add to the body of evidence that implicates differential losses in the operation of the two cone-opponent systems as the cause of changes in color perception in the retinal periphery.

Differential influence by rods on the two opponent pathways might also be a reason for the changing functional capabilities of the $L-M$ and $S-(L+M)$ systems with increasing retinal eccentricity. In an attempt to explain the variety of complex effects on color vision that are mediated by rods, the existence of different pathways has been postulated via which they can exert separate influences on the midget and small bistratified ganglion cells of the $L-M$ and $S-(L+M)$ systems, respectively [63]. The rod effects mediated by the midget ganglion cells, for example, have been shown to be faster acting and operational over a wider range of light levels [64]. It might be expected that, as luminance is decreased from photopic to scotopic levels, the influence of rods would become more significant. However, in as yet unpublished control studies, we have observed little change in the hue

or saturation versus eccentricity functions from mesopic (1.25 cd m^{-2}) to well into the photopic range (62.5 cd m^{-2}). Thus the importance of rods in our data remains undetermined.

B. Perceived Saturation and Hue Changes

While relative decreases in the functional capacity of the $L-M$ and S cone-opponent systems might account for a major proportion of the changes in color appearance that occur with increasing retinal eccentricity, there remain some differences between the behavior of perceived variations in hue and saturation. Desaturation of chromatic stimuli appears to be a frequent feature of color vision in the peripheral retina [2,4,12,21,22] but, in agreement with previous observations [4], the present study demonstrates that desaturation is not constant across color space. The pattern of variation in perceived saturation, though similar, is not identical to that observed for perceived shifts in hue. In certain regions there is little or no perceived shift in saturation, while in others, particularly midspectral greens, there are large shifts. The selective desaturation effect for green stimuli is a possible reason why such colors have been found to have a larger perceptible field size than other colors [12]. The other more distinctive difference between the variations in hue and saturation lies in their susceptibility to changes in stimulus size. Other studies have clearly demonstrated that color perception in the retinal periphery is greatly influenced by stimulus size [12]. Our studies show that there is a dissociation between perceived hue and saturation in the respect that changes in saturation are reduced with large peripherally presented stimuli, while those in hue remain largely unaffected by increases in stimulus size.

The difference observed between the effects of stimulus size on perceived hue and saturation is problematic when viewed in the context of previous studies. On the one hand, the fact that perceived saturation shifts are negated by increases in stimulus size supports the idea that changes in peripheral color vision are cortically imposed [38]. But in direct contradiction to this view, the persistence of perceived hue shifts, despite increases in stimulus size, supports the idea of retinally based changes in cone connectivity [36]. One possible reason for this discrepancy might be the fact that different aspects of color vision are being examined across these studies. In this study we are looking at variations in appearance of *suprathreshold* chromatic stimuli, while previously it has been the *sensitivity* of cone-opponent mechanisms to chromatic stimuli that has been addressed [38]. Recently, Solomon *et al.* [42] have conceded that there may well be some reduction in the quality of $L-M$ opponent signals in peripheral retina. They suggest this may be due partly to three factors: the temporal characteristics of the preganglionic cell synaptic circuits, the eccentricity-dependent increases in delay between center and surround responses, as well as a reduction in the overall number of cells showing overt opponent responses. At the same time, however, they stress that, despite this reduction in the quality of cone opponency in the periphery, there are no physiologically measurable differences in sensitivity between central and peripheral $L-M$ opponent cells [42]. Hence we might speculate that, while absolute *sensitivity*

to chromatic stimuli might be restored by adequate size scaling [38], the hue or color appearance of suprathreshold stimuli on the other hand might be affected to a greater extent by this loss of quality of the opponent signal. As our experimental observations here and elsewhere [10] indicate, this may not be restored simply by making the stimuli larger.

Other bases for the different behavior of perceived hue and saturation changes with respect to stimulus size also have to be considered. One possibility might be that perceived saturation changes are the result of additional influences exerted on the cone-opponent signals that are not exerted on the mechanisms that generate the hue shifts. Rod photoreceptors are a potential source of this influence, and their activity has been associated with the generation of perceived saturation changes right from the early investigations of color perception in the retinal periphery [1,2]. One thing that is clear is that rods appear to be able to exert a diverse range of influence on the chromatic signal via a number of different connective networks in the retina [63]. Several observations have specifically implicated rods in perceived changes in the saturation of chromatic stimuli. For example, desaturation effects have been found to be more prominent during the rod-mediated phase of dark adaptation [4,24] and can be reduced when surrounds of high luminance are used [65]. Negerer and colleagues [30] have also shown that following recovery from an intense bleaching stimulus, the perceived saturation of peripherally presented (eccentricity= 8°) chromatic stimuli is significantly shifted following the recovery of rod sensitivity. Perceived hue is not altered during this period. The influence of rods in the generation of perceived peripheral saturation shifts may also be via their suppression of cone activity [3,33,66–68]. Of particular relevance to this study is that the effects of rods on chromatic judgements are very much dependent upon stimulus size [5,69]. It has been predicted that the desaturation effects of rod intrusion should change significantly with size [4], and this is borne out by the data presented here. But while rods may be implicated in perceived saturation shifts in the peripheral retina, their influence on color perception may be much more complex and wide ranging. It should not be overlooked that the rods have also been shown to generate a wide range of changes in perceived hue that are also dependent upon the temporal as well as spatial parameters of the stimulus [5,20,26–28,63,64].

While the foregoing discussion has concentrated on retinal-based mechanisms, there also remains the possibility that the differences that exist between hue and saturation perception in the periphery are due to centrally (i.e., cortically) imposed limitations on processing. If the cortical magnification factors for hue and saturation differ, this would result in their being size scaled differently across the retina. A consequence of this would be that the rate of increase in stimulus size with eccentricity required to equate peripheral with foveal vision would be different for hue and saturation. This is essentially what we are observing in the data presented here—a difference in behavior with stimulus size. The notion that hue and saturation might possess different scaling factors is supported by the fact that the spatial scale of the visual sys-

tem is known to be very much dependent upon specific visual attributes and can vary widely between different psychophysical tasks [70]. For example, the spatial scale for the detection of motion varies very little with increasing retinal eccentricity [71], while that for $L-M$ chromatic patterns changes markedly [38]. Thus the differences in the behavior of perceived hue and saturation shifts with stimulus size may be a reflection of different processing pathways being involved in the analysis of these two aspects of chromatic stimuli, with each having their own particular scaling factor. Certainly, further experimentation will be necessary in order to quantify the scaling factors for hue and saturation. This may clarify the roles of retinal and cortically based mechanisms in the observed differences between perceived hue and saturation changes in the retinal periphery.

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REFERENCES

1. R. Lythgoe, "Dark-adaptation and the peripheral colour sensations of normal subjects," *Br. J. Ophthalmol.* **15**, 193–210 (1931).
2. J. D. Moreland and A. Cruz, "Colour perception with the peripheral retina," *Opt. Acta* **6**, 117–151 (1959).
3. B. Stabell and U. Stabell, "Rod and cone contributions to peripheral colour vision," *Vision Res.* **16**, 1099–1104 (1976).
4. B. Stabell and U. Stabell, "Peripheral colour vision: effects of rod intrusion at different retinal eccentricities," *Vision Res.* **36**, 3407–3414 (1996).
5. J. L. Nerger, V. J. Volbrecht, and C. J. Ayde, "Unique hue judgments as a function of test size in the fovea and at 20-deg temporal eccentricity," *J. Opt. Soc. Am. A* **12**, 1225–1232 (1995).
6. V. J. Volbrecht, J. L. Nerger, S. M. Imho, and C. J. Ayde, "Effect of the short-wavelength-sensitive cone mosaic and rods on the locus of unique green," *J. Opt. Soc. Am. A* **17**, 628–634 (2000).
7. M. Ayama and M. Sakurai, "Changes in hue and saturation of chromatic lights in the peripheral visual field," *Color Res. Appl.* **28**, 413–424 (2003).
8. M. Sakurai, M. Ayama, and T. Kumagai, "Color appearance in the entire visual field: color zone map based on the unique hue component," *J. Opt. Soc. Am. A* **20**, 1997–2009 (2003).
9. I. Abramov and J. Gordon, "Seeing unique hues," *J. Opt. Soc. Am. A* **22**, 2143–2153 (2005).
10. N. R. A. Parry, D. J. McKeefry, and I. J. Murray, "Variant and invariant color perception in the near peripheral retina," *J. Opt. Soc. Am. A* **23**, 1586–1597 (2006).
11. J. D. Moreland, "Peripheral colour vision," in *Handbook of Sensory Physiology*, Vol. VII/4 of Visual Psychophysics, J. Jameson and L. M. Hurvich, eds. (Springer, 1972), pp. 517–536.
12. I. Abramov, J. Gordon, and H. Chan, "Color appearance in the peripheral retina: effects of stimulus size," *J. Opt. Soc. Am. A* **8**, 404–414 (1991).
13. H. Knau and J. S. Werner, "Senescent changes in parafoveal color appearance: saturation as a function of stimulus area," *J. Opt. Soc. Am. A* **19**, 208–214 (2002).
14. J. Gordon and I. Abramov, "Color vision in the peripheral retina. II. Hue and saturation," *J. Opt. Soc. Am.* **67**, 202–207 (1977).
15. C. E. Ferree and G. Rand, "Chromatic thresholds of sensation from center to periphery of the retina and their bearing on color theory," *Psychol. Rev.* **26**, 16–41 (1919).
16. R. M. Boynton, W. Schafer, and M. E. Neun, "Hue-wavelength relationship measured by color-naming method for three retina locations," *Science* **146**, 666–668 (1964).
17. D. O. Weitzman and J. A. S. Kinney, "Effect of stimulus size, duration, and retinal location upon the appearance of color," *J. Opt. Soc. Am.* **59**, 640–643 (1969).
18. G. Wald, "Blue-blindness in the normal fovea," *J. Opt. Soc. Am.* **57**, 1289–1303 (1967).
19. R. W. G. Hunt, "Light and dark adaptation and the perception of color," *J. Opt. Soc. Am.* **42**, 190–199 (1952).
20. B. Stabell and U. Stabell, "Rod and cone contributions to change in hue with eccentricity," *Vision Res.* **19**, 1121–1125 (1979).
21. U. Stabell and B. Stabell, "Colour vision in the peripheral retina under photopic conditions," *Vision Res.* **22**, 839–844 (1982).
22. U. Stabell and B. Stabell, "Color-vision mechanisms of the extrafoveal retina," *Vision Res.* **24**, 1969–1975 (1984).
23. U. Stabell and B. Stabell, "Mechanisms of chromatic rod vision in scotopic illumination," *Vision Res.* **34**, 1019–1027 (1994).
24. B. Stabell and U. Stabell, "Effects of rod activity on color perception with light adaptation," *J. Opt. Soc. Am. A* **19**, 1249–1258 (2002).
25. U. Stabell and B. Stabell, "Effects of light and dark adaptation of rods on specific-hue threshold," *Vision Res.* **43**, 2905–2914 (2003).
26. P. W. Trezona, "Rod participation in the 'blue' mechanism and its effect on colour matching," *Vision Res.* **10**, 317–332 (1970).
27. S. Buck, R. Knight, G. Fowler, and B. Hunt, "Rod influence on hue-scaling functions," *Vision Res.* **38**, 3259–3263 (1998).
28. S. Buck, R. Knight, and J. Bechtold, "Opponent-color models and the influence of rod signals on the loci of unique hues," *Vision Res.* **40**, 3333–3344 (2000).
29. V. J. Volbrecht, J. L. Nerger, and C. J. Ayde, "Unique hue judgements in the peripheral retina as a function of stimulus size, duration and rod contribution," *Invest. Ophthalmol. Visual Sci.* **34**, 765–765 (1993).
30. J. L. Nerger, V. J. Volbrecht, and K. A. Haase, "The influence of rods on colour naming during dark adaptation," in *Normal and Defective Colour Vision*, J. D. Mollon, J. Pokorny, and K. Knoblauch, eds. (Oxford Press, 2003) pp. 173–177.
31. C. A. Curcio, K. A. Allen, K. R. Sloan, C. L. Lerea, J. A. Hurley, I. B. Klock, and A. H. Milam, "Distribution and morphology of the human photoreceptors stained with anti-blue opsin," *J. Comp. Neurol.* **312**, 610–624 (1991).
32. D. R. Williams, D. I. R. MacLeod, and M. M. Hayhoe, "Foveal tritanopia," *Vision Res.* **21**, 1341–1356 (1981).
33. A. L. Nagy and J. A. Doyal, "Red-green color discrimination as a function of stimulus field size in peripheral vision," *J. Opt. Soc. Am. A* **10**, 1147–1156 (1993).
34. C. Noorlander, J. J. Koenderink, R. J. den Ouden, and B. W. Edens, "Sensitivity to spatiotemporal colour contrast in the peripheral visual field," *Vision Res.* **23**, 1–11 (1983).
35. J. A. Van Esch, E. E. Koldenhoff, A. J. Van Doorn, and J. J. Koenderink, "Spectral sensitivity and wavelength discrimination of the human peripheral visual field," *J. Opt. Soc. Am. A* **1**, 443–450 (1984).
36. K. T. Mullen and F. A. A. Kingdom, "Differential distributions of red-green and blue-yellow cone opponency across the visual field," *Visual Neurosci.* **19**, 109–118 (2002).
37. K. T. Mullen, M. Sakurai, and W. Chu, "Does $L-M$ cone opponency disappear in the human periphery?" *Perception* **34**, 951–959 (2005).
38. C. Vakrou, D. Whitaker, P. V. McGraw, and D. J. McKeefry,

- “Functional evidence for cone-selective connectivity in the human retina,” *J. Physiol. (London)* **566**, 93–102 (2005).
39. I. J. Murray, N. R. A. Parry, and D. J. McKeefry, “Cone opponency in the near peripheral retina,” *Visual Neurosci.* **23**, 503–507 (2006).
 40. D. M. Dacey, “Circuitry for color coding in the primate retina,” *Proc. Natl. Acad. Sci. U.S.A.* **93**, 582–588 (1996).
 41. L. Diller, O. S. Packer, J. Verweij, M. J. McMahon, D. R. Williams, and D. M. Dacey, “*L* and *M* cone contributions to the midget and parasol ganglion receptive fields of macaque monkey retina,” *J. Neurosci.* **24**, 1079–1088 (2004).
 42. P. R. Martin, B. B. Lee, A. J. White, S. G. Solomon, and L. Rüttiger, “Chromatic sensitivity of ganglion cells in the peripheral primate retina,” *Nature* **410**, 933–936 (2001).
 43. S. G. Solomon, B. B. Lee, A. J. R. White, L. Rüttiger, and P. R. Martin, “Chromatic organization of ganglion receptive fields in peripheral retina,” *J. Neurosci.* **25**, 4527–4539 (2005).
 44. C. R. Ingling and B. Tsou, “Orthogonal combinations of the three visual channels,” *Vision Res.* **17**, 1075–1082 (1977).
 45. R. Stanikunas, H. Vaitkevicius, J. J. Kulikowski, I. J. Murray, and A. Daugirdiene, “Colour matching of isoluminant samples and backgrounds: a model,” *Perception* **34**, 995–1022 (2005).
 46. R. L. DeValois, I. Abramov, and G. H. Jacobs, “Analysis of response patterns of LGN cells,” *J. Opt. Soc. Am.* **56**, 966–977 (1966).
 47. A. M. Derrington, J. Krauskopf, and P. Lennie, “Chromatic mechanisms in lateral geniculate nucleus of macaque,” *J. Physiol. (London)* **357**, 241–265 (1984).
 48. M. A. Pitts, L. J. Troup, V. J. Volbrecht and J. L. Nerger, “Chromatic perceptive field sizes change with retinal illuminance,” *J. Vision* **5**, 435–443 (2005).
 49. V. C. Smith and J. Pokorny, “Spectral sensitivity of the foveal cone photopigments between 440 and 550 nm,” *Vision Res.* **15**, 161–171 (1975).
 50. T. Benzschwel, M. T. Brill, and T. E. Cohn, “Analysis of human color mechanisms using sinusoidal spectral power distributions,” *J. Opt. Soc. Am. A* **3**, 1713–1723 (1986).
 51. S. L. Guth, R. W. Massof, and T. Benzschwel, “Vector model for normal and dichromatic color vision,” *J. Opt. Soc. Am.* **70**, 197–211 (1980).
 52. J. Krauskopf, D. R. Williams, and D. W. Heeley, “Cardinal directions of color space,” *Vision Res.* **22**, 1123–1131 (1982).
 53. J. Carroll, M. Neitz, and J. Neitz, “Estimates of *L:M* cone ratio from ERG flicker photometry and genetics,” *J. Vision* **2**, 531–542 (2002).
 54. C. R. Ingling, “The spectral sensitivity of the opponent-color mechanisms,” *Vision Res.* **17**, 1083–1089 (1977).
 55. K. T. Mullen, “Color vision as a post-receptoral specialization of the central visual-field,” *Vision Res.* **31**, 119–130 (1991).
 56. T. N. Wiesel and D. H. Hubel, “Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey,” *J. Neurophysiol.* **29**, 1115–1156 (1966).
 57. D. M. Dacey, “Parallel pathways for spectral coding in primate retina,” *Annu. Rev. Neurosci.* **23**, 743–775 (2000).
 58. K. T. Mullen and F. A. A. Kingdom, “Losses in peripheral colour sensitivity predicted from ‘hit and miss’ post-receptoral cone connections,” *Vision Res.* **36**, 1995–2000 (1996).
 59. W. Paulus and A. Krogerpaulus, “A new concept of retinal color coding,” *Vision Res.* **23**, 529–540 (1983).
 60. D. M. Dacey, “The mosaic of midget ganglion cells in the human retina,” *J. Neurosci.* **13**, 5334–5355 (1993).
 61. D. M. Dacey and M. R. Peterson, “Dendritic field size and morphology of midget and parasol ganglion cells of the human retina,” *Proc. Natl. Acad. Sci. U.S.A.* **93**, 582–588 (1992).
 62. S. G. Solomon, P. R. Martin, A. J. R. White, L. Rüttiger, and B. B. Lee, “Modulation sensitivity of ganglion cells in peripheral retina of macaque,” *Vision Res.* **42**, 2893–2898 (2002).
 63. S. Buck, “What is the hue of rod vision?” *Color Res. Appl.* **26**, S57–S59 (2001).
 64. R. Knight and S. L. Buck, “Time-dependent changes of rod influence on hue perception,” *Vision Res.* **42**, 1651–1662 (2002).
 65. I. Abramov, J. Gordon, and H. Chan, “Color appearance across the retina: effects of a white surround,” *J. Opt. Soc. Am. A* **9**, 195–201 (1992).
 66. I. Lie, “Dark adaptation and the photochromatic interval,” *Doc. Ophthalmol.* **17**, 411–510 (1963).
 67. L. Spillmann and J. E. Cordon, “Photochromatic interval during dark adaptation and as a function of background luminance,” *J. Opt. Soc. Am.* **62**, 182–185 (1972).
 68. N. S. Peachey, K. R. Alexander, and D. J. Derlacki, “Spatial properties of rod cone interactions in flicker and hue detection,” *Vision Res.* **30**, 1205–1210 (1990).
 69. J. L. Nerger, V. J. Volbrecht, C. J. Ayde, and S. M. Imhoff, “Effect of the *S* cone mosaic and rods on red/green equilibria,” *J. Opt. Soc. Am. A* **15**, 2816–2826 (1998).
 70. D. Whitaker, P. Makela, J. Rovamo, and K. Latham, “The influence of eccentricity on position and movement acuities as revealed by spatial scaling,” *Vision Res.* **32**, 1913–1930 (1992).
 71. D. M. Levi, S. A. Klein, and P. Aitsebaomo, “Detection and discrimination of the direction of motion in the central and peripheral vision of normal and amblyopic observers,” *Vision Res.* **24**, 789–800 (1984).