

Variant and invariant color perception in the near peripheral retina

Neil R. A. Parry

Vision Science Center, Manchester Royal Eye Hospital, Manchester, M13 9WH, UK

Declan J. McKeefry

Department of Optometry, School of Life Sciences, University of Bradford, Bradford, BD7 1DP, UK

Ian J. Murray

Faculty of Life Sciences, University of Manchester, Manchester, M13 9PT, UK

Received September 23, 2005; revised January 10, 2006; accepted January 22, 2006; posted February 7, 2006 (Doc. ID 64952)

Perceived shifts in hue that occur with increasing retinal eccentricity were measured by using an asymmetric color matching paradigm for a range of chromatic stimuli. Across nine observers a consistent pattern of hue shift was found; certain hues underwent large perceived shifts in appearance with increasing eccentricity, while for others little or no perceived shift was measured. In separate color naming experiments, red, blue, and yellow unique hues were found to be correlated with those hues that exhibited little or no perceptual shift with retinal eccentricity. Unique green, however, did not exhibit such a strong correlation. Hues that exhibited the largest perceptual shifts in the peripheral retina were found to correlate with intermediate hues that were equally likely to be identified by adjacent color naming mechanisms. However, once again the correlation was found to be weakest for the green mechanism. These data raise the possibility that perceptually unique hues are linked to color signals that represent the most reliable (minimally variant) chromatic information coming from the retina. © 2006 Optical Society of America

OCIS codes: 330.1720, 330.5510.

1. INTRODUCTION

Human color perception is markedly different in the peripheral retina compared with that experienced within the foveal region. It has long been appreciated, for example, that when a colored stimulus is moved from the fovea to more eccentric retinal positions, there are changes in its perceived hue and saturation.¹ These shifts in perception have been clearly demonstrated in color matching experiments that have revealed changes in the size and shape of the spectral locus with increasing retinal eccentricity.^{2–5} In addition, other studies have shown that our perception of basic color categories and unique hues is very different in the retinal periphery.^{6–12} Yet while there is strong evidence in favor of altered color perception in the retinal periphery, it is not entirely clear what the underlying cause(s) may be. One view is that shifts in peripheral color vision constitute some fundamental reorganization of cone inputs into color opponent mechanisms. Early psychophysical evidence tended to favor this possibility, with different regions of the retina exhibiting different kinds of color vision: trichromacy in the central retina and dichromacy in the intermediate regions, with the far periphery being monochromatic.^{1,3,13–15} The idea that color vision may be configured differently in the eccentric retina also finds resonance with modern anatomical studies, which have raised the possibility of a change in the nature of cone inputs to peripheral ganglion cells.¹⁶ However, this is not universally accepted.¹⁷ Although evidence for a funda-

mental change in the neural circuitry of color vision in the peripheral retina remains inconclusive, what does seem apparent is that there are a number of other factors that may contribute to our altered perception of color in the retinal periphery. Recent behavioral studies have focused on the relative changes that occur between the L–M- and S-cone opponent mechanisms as a function of retinal eccentricity. What has emerged from these studies is that color vision mediated by the L–M system is a special feature of the central visual field, which declines in efficacy in the peripheral retina. Color vision mediated by the S-cone system, on the other hand, is comparatively more resistant to constraints imposed by increasing retinal eccentricity.^{18–20}

Another factor that may affect color vision in the retinal periphery is the increasing influence of rods. Rods share a common pathway with S cones and also have input to L and M ganglion cells,^{21–23} their increased predominance in the retinal periphery making them more likely to interact with cones.^{24–27} In general, rod influence appears to lead to a desaturation of colored stimuli as well as to bring about a complex range of changes in perceived hue,²⁸ which may occur across many color categories.^{10–12,25,29,30} The influence of rods on the appearance of peripheral color stimuli is further complicated by the fact that their effects appear to be dependent on a variety of stimulus parameters such as intensity and temporal presentation.^{30,31}

Yet another school of thought holds that altered color

vision in the retinal periphery is simply the result of poorer sampling by the cone receptors. Therefore, as long as certain parameters such as intensity and, particularly, stimulus size, compensate for this reduced sampling efficiency, then color vision in the periphery is similar to that experienced in the foveal region. This would seem to be borne out by studies that show a restoration of spectral sensitivity, wavelength discrimination, and color appearance in the peripheral retina when test stimuli are appropriately scaled for eccentricity.^{7,32,33} In fact this dependency of color appearance on stimulus size led Abramov and colleagues to introduce the concept of “perceptive field size,” the minimum size of the test stimulus that is necessary to make the experience of color provided by the peripheral stimulus comparable with that experienced foveally.⁷

The foregoing indicates that the perception of color of peripherally presented stimuli is the result of complex physical and physiological interactions. In this series of experiments, we were interested in exploring the relationship between the influence of retinal eccentricity on the perception of color and chromatic processing mechanisms. It is known that, subcortically at least, color information is processed along L–M- and S-cone opponent pathways, which receive input from the long-, middle-, and short-wavelength-sensitive cones (L, M, and S cones) in the retina.³⁴ However, when it comes to accounting for certain phenomenological aspects of color perception, this cone opponent model does not prove to be very satisfactory. For example, it cannot account for color appearance. Colors that are typically described as being representative examples of pure red, green, blue, and yellow, the so-called unique hues, do not coincide with colors that isolate the activity of the L–M- and S-cone opponent systems.^{35,36} This discrepancy between the initial neurophysiological processing of color information by the visual system and the emergence of basic color sensory experience is often explained by a reorganization of color processing at some “higher,” presumably cortical, level.³⁷ Yet the emergence and status of unique hues remain puzzles.³⁸

To explore these issues, the stimuli utilized in these experiments sampled hues in DKL color space. Such a space is useful in that it permits the generation of colors that modulate along different chromatic axes, some of which have physiological significance. In particular this color space identifies two cardinal axes that isolate the L–M- and S-cone opponent mechanisms.^{35,39} However, the exact localization of these axes is neither straightforward nor without controversy, and care should be taken in relating results from particular color spaces directly with physiology.^{40,41} With this caveat in mind, we have utilized this color space primarily because it has been employed in earlier psychophysical experiments that have identified particular chromatic axes that coincide with unique hues.³⁶ In addition, this color space has the added advantage of allowing the examination of a wide range of isoluminant chromatic stimuli, incorporating spectral as well as nonspectral hues. Previous studies have tended to concentrate on spectral wavelengths,^{2,28} in certain cases on discrete wavelengths that coincide with the unique hues.^{10,42} Although this paper concentrates on characterizing shifts in perceived hue with retinal eccentricity, con-

current measurements of saturation shifts were also made. Shifts in hue and saturation have often been found to occur in tandem as chromatic stimuli move to more peripheral retinal locations and, as a result, have tended to be confounded with one another.² We find that when perceived shifts in hue with retinal eccentricity are measured, there is a pattern of change across color space that is highly repeatable for different individuals. Whilst there appear to be marked shifts in perceived hue in some regions of color space, in others there is little or no shift. Furthermore, these maxima and minima are closely related to color appearance mechanisms.

2. METHODS

A. Stimuli

For most of the experiments described here, the stimuli consisted of a pair of circular colored patches on a uniform gray background. One of these (the probe) was presented close to fixation, and the other (the test) was presented more peripherally. The stimuli were generated by using purpose-built software to drive a VSG 2/5 video graphics card (Cambridge Research Systems Ltd., Rochester, UK) on a high-resolution graphics monitor (Sony GDM520) that subtended $26.3^\circ \times 32.75^\circ$. Chromaticity of the stimuli was defined in terms of vectors in a modified version of the MacLeod–Boynton chromaticity diagram described by Derrington *et al.*³⁹ In this color space, the angle ϕ depicts a chromatic axis within which modulation along the 0° – 180° axis corresponds to the L–M cardinal axis and modulation along the 90° – 270° axis coincides with the S-cone cardinal axis. Note that ϕ is the direct equivalent of azimuth in DKL space. These cardinal axes are illustrated in CIE (1931) color space in Fig. 1(a). Saturation was defined as the length along a straight vector from the background [CIE $(x,y)=(0.31,0.316)$, $Y=12.5$ cd m⁻²] in a particular direction, so that hues of equal saturation formed a circle in CIE (1931) color space, and unity saturation approached the maximum that would allow all stimuli to fall within the gamut of the monitor’s phosphors. The x and y chromaticity coordinates when $\phi=0$ and saturation=1 were 0.3819 and 0.2866, respectively. The chromaticity of each stimulus could be varied in either hue or saturation by moving through color space in the directions shown in Fig. 1(b). In addition the luminance of the stimulus could be varied (by ± 0.01 cd m⁻²), although for all subjects this parameter was found to show little appreciable variation across color space. Stimuli also varied in size and in retinal eccentricity but were always presented in the nasal visual field.

Note that, in these experiments, mean luminance of the probe stimulus was kept at a constant 12.5 cd m⁻². In a separate study, we are looking at the effects of large and small departures from both nominal and subjective isoluminance. For the current, basically phenomenological, study, we have decided not to vary the luminance of the probe stimulus. We have established that the effects described here are not dependent on this restriction.

The monitor was calibrated by using an OptiCal probe (Cambridge Research Systems Ltd., Rochester, UK), which was itself calibrated against a PR650 Spectrascan SpectraColorimeter (Photo Research Inc., Chatsworth,

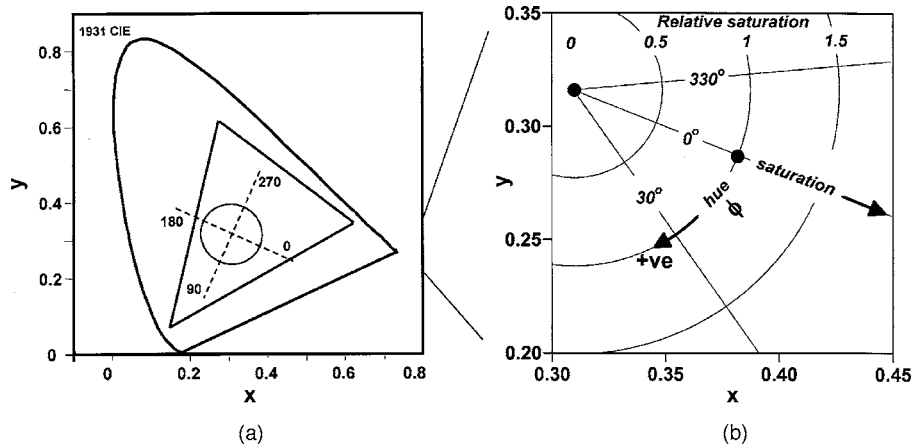


Fig. 1. (a) CIE (1931) chromaticity diagram showing the triangular gamut of the monitor's phosphors and the location of the hue circle (saturation=1) employed in these studies. The cardinal chromatic axes (0° , 90° , 180° , and 270°) are also indicated. (b) Enlarged section of the chromaticity diagram to show the direction of movement through color space when hue and saturation are altered. The concentric circles indicate the baseline saturation of unity together with higher and lower saturations (1.5 and 0.5). The actual saturation maximum depended on chromatic axis. The solid symbols depict the background chromaticity ($x=0.31$, $y=0.316$) and the 0° (cardinal red) stimulus ($x=0.3819$, $y=0.2866$). Saturation of this stimulus was changed by moving along the 0° vector. 30° and 330° vectors are also shown.

Calif.) in the following manner. The OptiCal software contains correction factors (C_r , C_g , and C_b) that compensate for intrinsic errors in sensitivity that the instrument has for the red, green, and blue CRT phosphors. These errors typically mean that following gamma correction input, x , y , and Y CIE (1931) values do not correspond to outputs measured by the PR650 from the CRT. The corrected luminance is achieved by multiplying the correction factor by the measured luminance. Initially, gamma functions were derived with high gray scale resolution and linear interpolation, and C_r , C_g , and C_b were set to unity (their default values). The software was then asked to display a CIE (1931) (x, y, Y) stimulus of (0.31, 0.316, 12.5), and its actual chromaticity was measured with the PR650. The R, G, and B voltages were noted, and the stimulus was then adjusted in x, y , and Y directions until it was correct according to the PR650. Each original R, G, and B gun voltage was divided by the adjusted value, which gave us new correction factors that were then employed in the final calibration. This method gives very high reliability within the range of stimuli used in this experiment, while still permitting rapid calibration. The cone contrasts produced by these stimuli were calculated by using the Judd modified values (x', y', Y') values. X', Y' , and Z' tristimulus values were then used in conjunction with cone fundamentals⁴³ to obtain the magnitude of cone excitation for each component color from which modulation for each cone (L_c, M_c , and S_c) was calculated.

B. Asymmetric Color Matching Task

To measure the perceived changes in hue that take place when stimuli are shifted to eccentric retinal locations, we employed an asymmetric color matching paradigm. In this task, a 1° diameter parafoveal probe stimulus was presented in the nasal visual field at an eccentricity of 1° for a period of 380 ms (see Fig. 2). Simultaneously a test stimulus was presented at a greater eccentricity. The subjects' task was to manipulate the chromaticity of the test so that it matched the probe. Viewing distance was always 50 cm, and a small black fixation mark was pro-

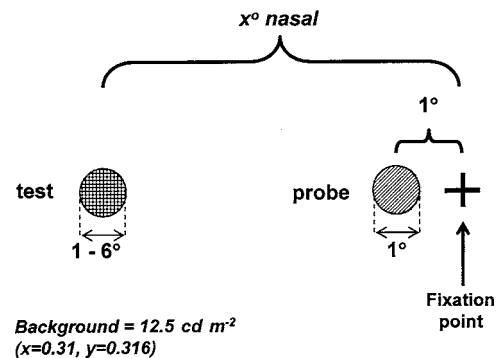


Fig. 2. Stimulus configuration. The fixation point was permanently displayed. Parafoveal probe and eccentric test spots appear simultaneously for 380 ms. Stimulus size and eccentricity were constant for all probe stimuli but in some experiments were varied for tests that were presented at more peripheral points in the nasal visual field.

vided. Viewing was monocular, and 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. Two matching paradigms were employed; one depended on "same/different" responses, while the other used a method of adjustment to generate matches between test and probe stimuli.

1. Same/Different Paradigm

In this experiment we tested a range of parafoveal probe chromaticities, with mean luminance of 12.5 cd m^{-2} , constant saturation of 0.5, and variable chromatic axis ϕ [see Fig. 1(b)]. For each value of ϕ , we placed the test stimulus at various eccentricities, from 2° to 24° . In a single run, one probe hue and one test eccentricity were employed. Between 10 and 16 test hues were presented, each ten times, randomly mixed. The subject's task was to judge in his or her own time whether the two stimuli appeared to be the same color, responding "same" by pressing a lever in one direction and "different" by pressing it in the other. The objective was to derive a matching function ($p[\text{same}]$)

versus probe chromatic axis (ϕ), where p [same] is the proportion of stimuli reported by the observer as being of the same hue).

Before each trial the range of probe hues for each condition was chosen so that a clear maximum was flanked by values close to zero; typical step sizes (i.e., changes in ϕ) were approximately 3° . After the response was made, there was a pause of 500 ms before the next stimulus pair were presented. Typical response time was about 500 ms, so that each run took between 2.5 and 5.5 min to complete. The size of the test stimulus was varied systematically with eccentricity—see the individual results for these values.

2. Method of Adjustment

In this experiment the subject had free control over the hue, saturation, and luminance of the peripheral test stimulus. As before, a range of probe hues was presented with a test hue of greater eccentricity. Most experiments were done with the test stimulus at a nasal eccentricity of 18° and a diameter of 3° , although we did investigate other eccentricities and sizes. The parafoveal probe saturation was 0.5, and luminance was 12.5 cd m^{-2} . After a pair of stimuli were presented, the subject adjusted one of the three test parameters, rotating hue by $\pm 5^\circ$, changing saturation by ± 0.2 , or changing luminance by $\pm 0.01 \text{ cd m}^{-2}$. Therefore there were six possible responses, for which the subject was provided with three levers. After a single adjustment, there was a 500 ms interval before the new pair were presented. Once the subject was satisfied that the two stimuli were matched for all three parameters, he or she pressed a key that advanced the hue of the probe stimulus by 15° . The matching procedure was then repeated, starting with the last set test stimulus. The experiment was concluded when 25 probe hues had been tested, from 0° to 360° in 15° steps. The 0° and 360° presentations were repeats of the same stimulus, made so as to ensure that the adaptational state of the subject did not vary across the time course of the experiment. Usually the differences between the two settings did not vary by more than ± 1 Standard Deviation (sd). Typically each run took about 20–30 min to complete. In this paper we concentrate mainly on the hue data; the basic saturation data are presented here but will be dealt with more comprehensively in a separate paper.⁴⁴ The results are presented in terms of magnitude of the shift as a function of probe hue angle. In all experiments clockwise rotations in color space are designated as positive and anticlockwise rotations as negative.

C. Color Naming Task

In this experiment a single (unpaired) eccentric test stimulus was flashed for 380 ms, and the subject was required to name the color of the stimulus. He or she had four choices: red, blue, green, or yellow. Twenty one different chromatic axes from $\phi=0^\circ$ to $\phi=360^\circ$ were presented (in steps of 18°), and each was seen between 10 and 20 times. Presentation of these 210 to 420 stimuli was randomized. 500 ms after the subject's response, the next stimulus was presented, and each run took between 10 and 20 min to complete. For most of the data presented here, we employed a 3° diameter stimulus at 18° eccen-

tricity, with saturation of 0.5. The results were analyzed by deriving four color naming functions p [red], p [blue], p [green], and p [yellow], where p [color] was the proportion of times that a particular test hue was called that color. Unique red, blue, green, and yellow were defined as the central maxima of these functions. Another group of colors, which we have called nonunique hues, corresponds to specific axes in color space that are equally likely to be identified by adjacent color naming mechanisms.

D. Subjects

Nine color normal subjects participated in both the method of adjustment asymmetric color matching task and the color naming task, comparing eccentricities of 1° and 18° in the former and testing at 18° for the latter. There were four males and five females, all of whom had normal color vision, and best-corrected acuity of 6/6 or better. They viewed the stimuli with normal pupils. Mean (± 1 sd) age was 33.8 y (9.6) yr. Three of the male subjects were the authors, who also participated in the same/different asymmetric color matching task and other control studies. The six other subjects were naive to the precise nature of the investigation, but all were well-practiced psychophysical observers.

3. RESULTS

A. Asymmetric Color Matching

In initial experiments we were interested in how perceived stimulus hue was affected by retinal eccentricity, and we employed the “same/different” asymmetric color matching paradigm to measure these shifts for different hues in color space. In Fig. 3 these shifts are plotted in terms of the vector rotation needed to make the peripherally presented test stimulus match the probe stimulus placed at 1° nasal to the fovea. As can be observed, the hue shifts generally increase with increasing eccentricity but the magnitude of hue shift as a function of retinal eccentricity is not the same for all hues, with some chromatic axes appearing to undergo much larger perceived shifts than others. Extra data were collected around these regions of maximum and minimum shift.

When the data are plotted as a function of chromatic axis, as in Fig. 3(b), a more regular pattern of perceived hue shift can be observed across color space. The data exhibit prominent peaks and troughs, indicating the areas of color space where the maximum shifts in perceived hue occur. In essence, the shifts in hue with eccentricity can be simply characterized as being toward either blue or yellow. In the pink–purple region of color space ($\phi=0^\circ$ to 90°), a negative (anticlockwise) rotation of the test stimulus hue vector is required in order to make a match with the more centrally located test stimulus. This means that the more peripheral test stimulus has to be made more pink in order to counteract its perceived shift toward blue. The magnitude of this shift appears to reach a maximum between 45° and 70° in this color space. In the blue–green region ($\phi=130^\circ$ to 165°), the peripheral stimulus requires a positive (clockwise) rotation of the hue vector in order to match the central probe stimulus. Once again this indicates that the more eccentrically located test stimulus is being perceived as more blue and consequently has to be

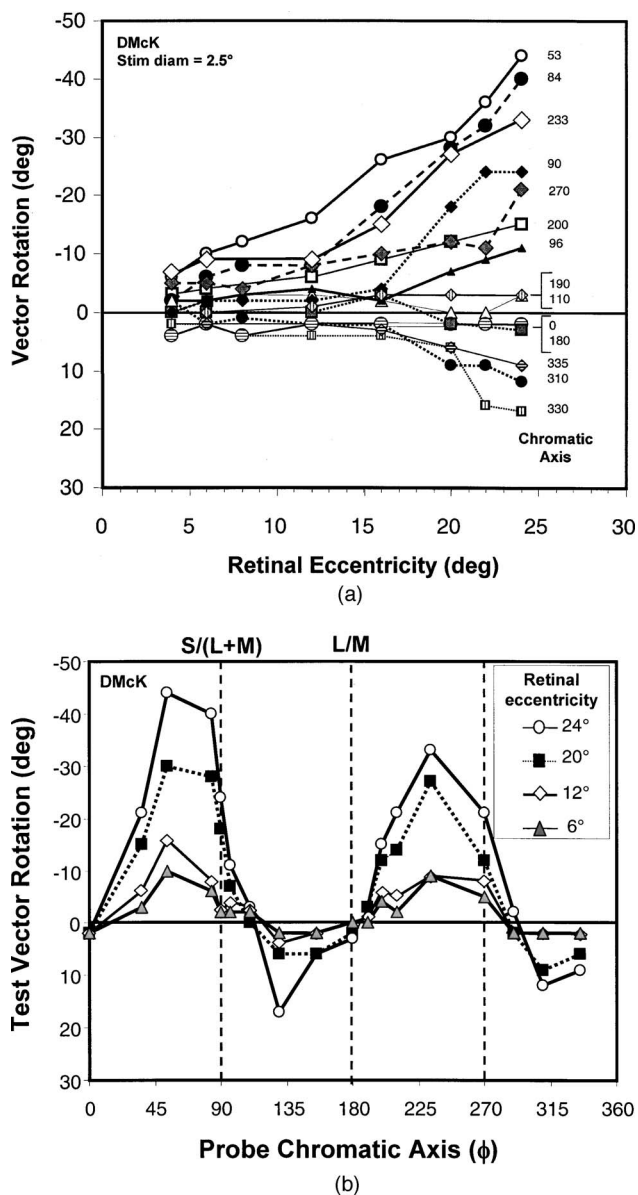


Fig. 3. Perceived hue shift as a function of eccentricity and probe chromaticity for subject DMK. (a) Hue shift as a function of eccentricity, measured by using the same/different paradigm. Each curve depicts the eccentricity function for a single probe chromaticity (see the chromatic axes at right). The y axis indicates the amount that the vector of the test stimulus had to be rotated in order to maximally match the probe's hue. Positive rotation indicates a clockwise movement through color space, so that, for example, when the 24° eccentricity probe stimulus had a hue angle of 330°, the test spot's hue angle was rotated by 16° to 346°. Not all of the chromatic axes tested have been plotted, in order to maintain clarity. (b) The same data (for four retinal eccentricities only) are plotted as a function of chromatic axis.

made greener in order to produce a match. In the second half of the color circle ($\phi=180^\circ$ to 360°), the perceived shifts in hue are toward yellow. In the green region of color space ($\phi=220^\circ$ to 260°), once again large negative rotations are required for matching, i.e., the peripheral test stimulus has to be made more green-blue in order to counteract the tendency for it to be perceived as yellow. Smaller positive rotations are required in the orange-pink region ($\phi=290^\circ$ to 360°).

Some peripheral test stimuli require little or no rotation away from the probe hue in order to generate a match in the central 25° of the retina. These minimum perceived shifts in hue are indicated by the zero crossing points of the function in Fig. 3(b) and occur at four regions in color space. The first zero crossing occurs in the pink region ($\phi=0^\circ$ to 10°), the second in the blue ($\phi=110^\circ$ to 120°), the third in the green ($\phi=180^\circ$ to 190°), and the last in the yellow ($\phi=290^\circ$ to 300°).

In all the experiments described herein, we have fixed the parameters of the near target and varied those of the more peripheral one. In control experiments, when we reversed this convention, the results mirrored those described here.

B. Intrasubject and Intersubject Variability

We wished to ascertain to what extent the pattern of perceived shifts in stimulus hue with retinal eccentricity, observed for a single subject (DMK) in Fig. 3, was a general feature of the wider color normal population. To this end we tested an additional eight subjects using an asymmetric color matching paradigm that incorporated the method of adjustment (see Subsection 2.B.2). This technique was faster and produced similar and repeatable hue shift functions to those in the same/different paradigm [see Fig. 4(a) for DMK's method of adjustment data].

Figure 4(b) shows the individual hue shift data for the eight other subjects who took part in the study, and Fig. 4(c) shows the average of these functions. On the whole the individual patterns appear to conform to a similar pattern of hue shift across color space, with large perceived shifts in color appearance for colors in the pink-purple region of color space ($\phi=45^\circ$ to 70°) and in the green-yellow region ($\phi=220^\circ$ to 260°). In addition to regions of large perceptual shifts, there are also certain axes in color space for all individuals that undergo minimal perceptual distortion. Figure 4(c) also shows the averaged saturation functions for the nine subjects. This aspect of the study is examined in more detail in a companion paper.⁴⁴ However, it is worth noting here that the variation seen in saturation does not correspond to the hue shift effect.

C. Size Control Experiment

While the pattern of perceived color shifts is consistent across different subjects, the possibility remains that these shifts are due simply to the size of the test stimulus, which perhaps has not been made large enough for "normal" color perception. In fact, as stated above, many studies have argued that color vision is size scaled, meaning that if peripheral color stimuli are simply made big enough, then perception of a full range of hues is possible in the retinal periphery.^{6,7} In a control experiment, we employed the same/different procedure to examine how asymmetric color matches varied as a function of test stimulus diameter for hues from two regions of color space [pink ($\phi=60^\circ$) and green ($\phi=240^\circ$)] that were perceived to undergo large shifts in color appearance with retinal eccentricity. Figure 5 shows the matching functions for two subjects and clearly indicates that the hue rotations required to produce a match with a more centrally placed (1°) probe stimulus are not affected by vary-

ing the stimulus size. The altered perception of color for the peripheral stimulus occurs for the largest field sizes and would seem to indicate that making the peripheral stimulus bigger does not make color vision in the periphery exactly fovealike.

D. Color Naming

What is interesting from the color matching data shown in Fig. 4 is that the maximum and minimum shifts in hue that occur with increasing retinal eccentricity are not coincident with the axes that isolate L-, M-, and S-cone in-

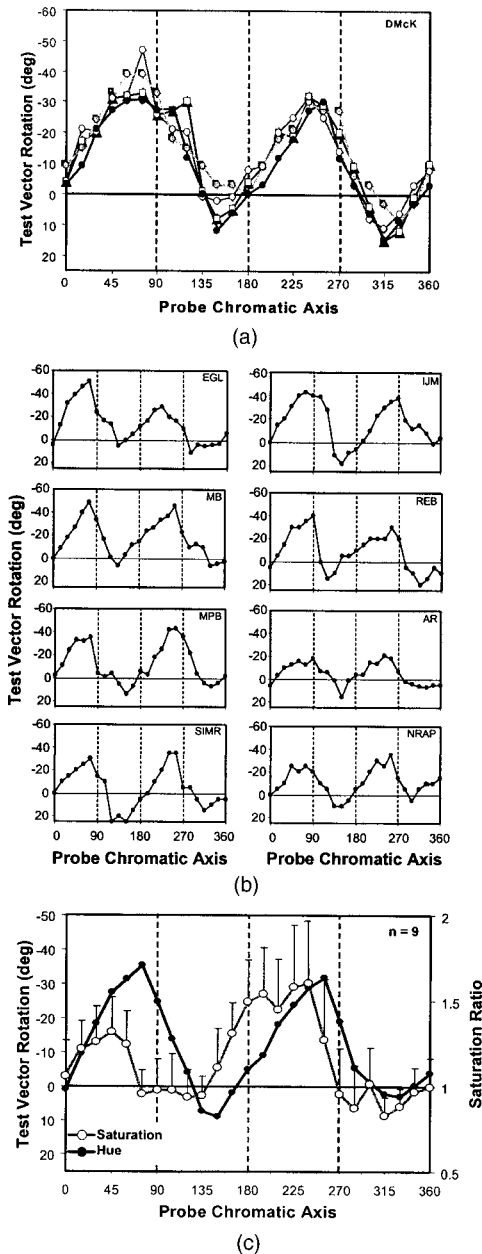


Fig. 4. (a) Hue shift as a function of probe hue angle; four successive runs showing within-subject variability in the same subject as that for Fig. 3 (DMK). (b) Hue shift as a function of probe hue angle measured in eight other subjects, using the same size and eccentricity as those in (a). (c) Mean of data in 4(a) and 4(b) \pm 1 sd. The graph also shows the simultaneously measured saturation function (mean of nine observers). The size is 3° , and the eccentricity is 18° nasal.

put to the opponent mechanisms. Instead, the regions of color space that were perceived invariant with retinal eccentricity seemed to be more closely associated with those chromatic axes that had been previously identified as the loci of so-called unique hues.³⁶ Unique hues can be defined as basic color sensations that appear phenomenologically unmixed or pure.⁴⁵ To explore this potential link between the peripherally invariant hues and those colors that could be identified as unique hues, we carried out color naming experiments on all of the observers who took part in the peripheral color matching experiments. These experiments were performed with test stimuli at the same nasal retinal eccentricity (18°) and of the same diameter (3°) as those used in the previous matching experiments. Four typical color naming functions are shown in Fig. 6(a) and are similar to color appearance mechanisms that have been described previously.³⁶

The group-averaged ($n=9$) hue scaling functions are shown in Fig. 6(b). In addition to localizing the unique hues (solid curves), the color naming data also enable us to identify other specific axes, which we have defined as “nonunique” hues (dotted curves). These were hues that any individual was equally likely to allocate to either of two adjacent color categories in color space and are indicated by the crossovers of the functions at the 50% level.

Using the data obtained during the course of the previous peripheral color matching experiments, we were also able to identify a number of key points on individual functions. These points specified the axes in color space at which the test stimuli were perceived to undergo the maximum positive and negative rotational shifts [solid curve in Fig. 6(c)] and those axes that showed minimal or no perceptual shift with retinal eccentricity (i.e., the zero crossings of the function, indicated by the dotted lines). To gauge the degree of correlation between the unique and nonunique hues identified by the color scaling experiments and the hues of maximum and minimum perceived variation in the color matching experiments, we plotted the results from these two experiments in Fig. 7.

In Fig. 7(a) the chromatic axes identified as the red, blue, green, and yellow unique hues are plotted against those points that were identified as being invariant with retinal eccentricity in the color matching experiments. The data points show the correspondence for all nine subjects between the color naming and the color matching experiments. If there were an exact correspondence between these two independent measures of chromatic perception, then all points would fall on a line of slope = 1 going through the origin. In Fig. 7(b) we have plotted the mean values of our nine subjects for the zero hue shift versus the unique hue comparisons as well as those for the maximum hue shift versus the nonunique hue locations. There appears to be a close degree of correlation between unique red, blue, and yellow and the corresponding invariant hues from the color matching experiment. However, the correlation between unique green and its corresponding zero crossing from the matching data is less convincing. Table 1 shows the *t*-statistics for these comparisons. For the nonunique hues and the hue shift maxima, there is a close correlation between the nonunique hues at the crossovers of red–blue and yellow–red naming functions, and their respective hue shift maxima and *t*-testing show

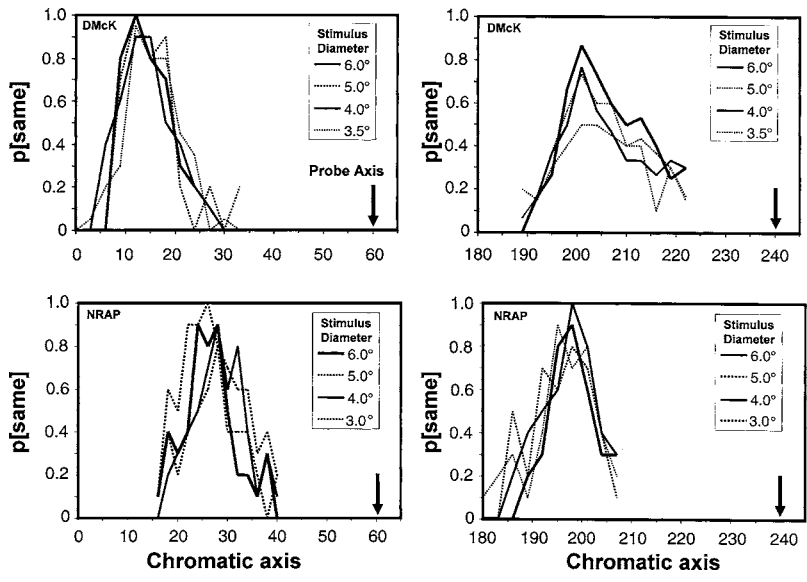


Fig. 5. Raw $p[same]$ functions for two subjects and two selected probe chromaticities (see the arrows) to show the independence of these functions from test size.

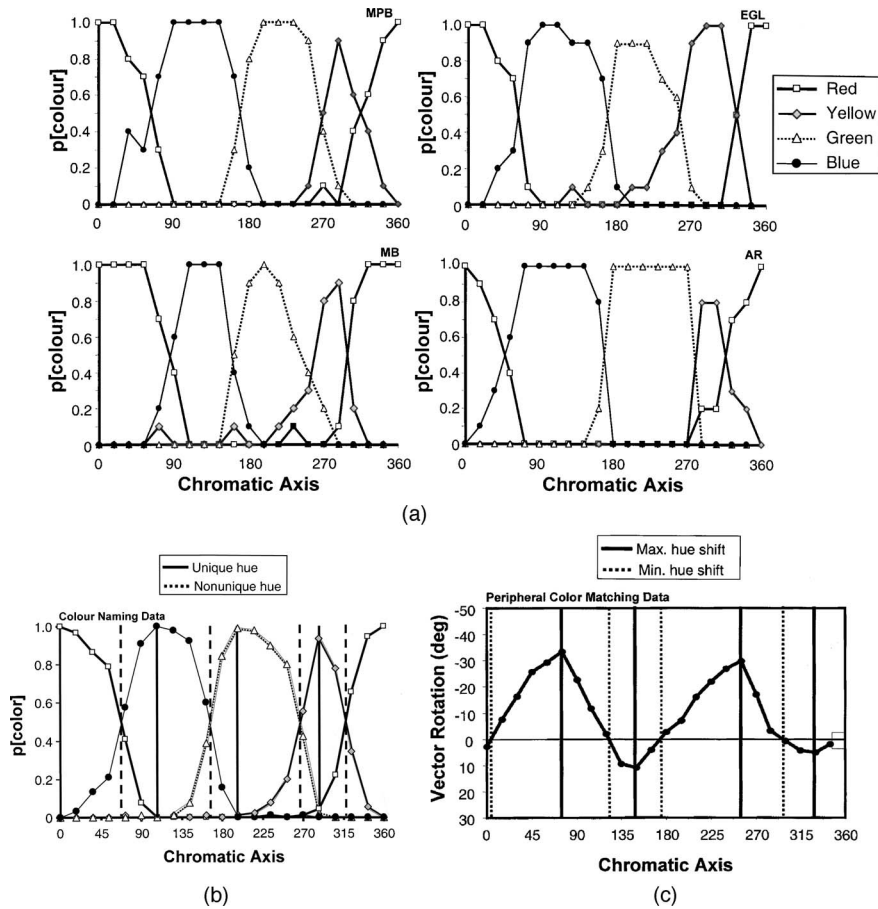


Fig. 6. (a) Color naming data for four representative subjects; results of a four-alternative forced choice experiment in which each of 21 test chromaticities was presented randomly 10–20 times. (b) Mean of color naming data for all nine observers presented in (a). (c) Mean color matching data, taken from Fig. 4(c), for comparison with (b).

them to be not significantly different from one another (see Table 1). This is in comparison with the nonunique hues located at the crossovers of the green naming function with blue and yellow, which are found to be signifi-

cantly different from each other. Note that we have not made a Bonferroni correction to these eight t -tests. For most combinations the data fail the conventional t -test ($\alpha=0.05$), indicating that for these cases we can accept

the null hypothesis that there is no difference between their means. In the cases where we reject the null hypothesis, making the *t*-test more conservative would make no difference to this decision.

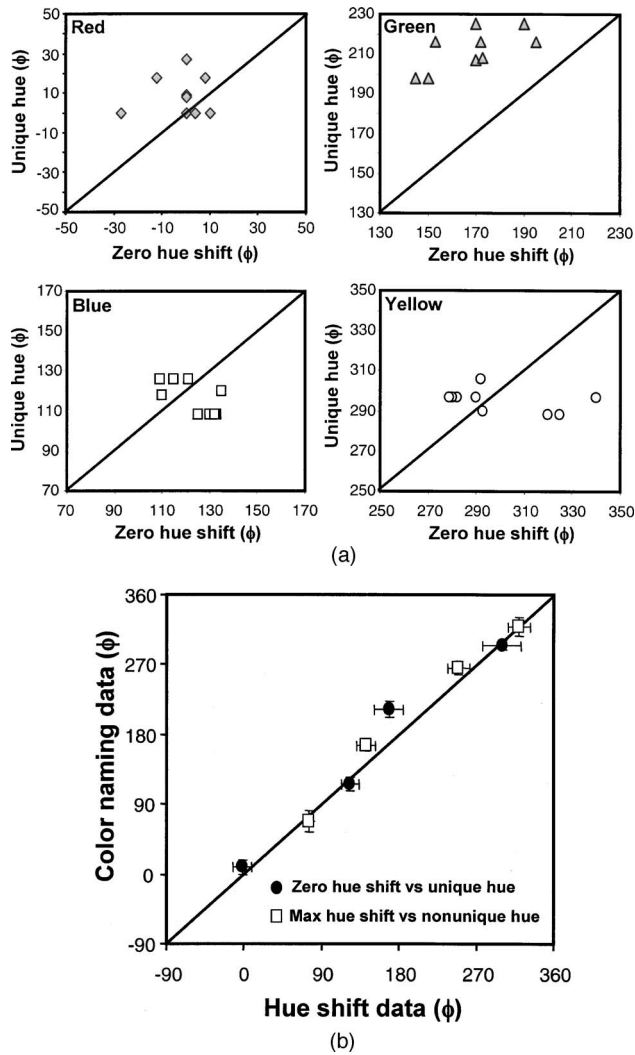


Fig. 7. (a) Correlation between zero crossings of the color matching functions in Figs. 4(a) and 4(b) (*x* axis) and red, green, blue, and yellow unique hues taken from Fig. 6(a) (*y* axis). Data points for the nine subjects are shown in each panel. (b) Correlation between the zero and maximum hue shifts in Figs. 4(a) and 4(b) (*x* axis) and the unique and nonunique (50% crossover points) in Fig. 6(a). The data represent the mean (± 1 sd) of nine subjects' data.

4. DISCUSSION

The central finding of this study is that, as colored stimuli fall on increasingly peripheral regions of the retina, hue shifts are perceived that are not uniform across color space. While certain hues undergo very noticeable shifts in their appearance, others remain largely invariant with increasing retinal eccentricity. Hues that are perceived as being invariant with retinal eccentricity were found, with the exception of green, to be correlated with unique hues. Conversely, those colors that exhibit the largest shifts in hue with retinal eccentricity correspond closely to chromatic axes that were equally likely to be identified by adjacent color appearance mechanisms in color space. This link with color appearance mechanisms is an interesting one, as it suggests that variant and invariant chromatic information coming from the retina might form a basis for higher order color perception. We also found that the chromatic axes at which stimuli undergo maximum and minimum perceptual shifts are not coincident with those that isolate L-, M-, and S-cone input to the second stage opponent mechanisms. This finding echoes earlier studies that have demonstrated a noncorrespondence between unique hues and cone opponent axes,³⁴ but we are wary of overinterpreting the significance of this finding in the light of potential limitations of the color space that we have employed. Another important observation is the lack of correspondence between the hue and saturation maxima—this is considered in more detail in another paper.⁴⁴

A. Perceived Hue Shifts in the Peripheral Retina

Quantitatively the perceived hue shifts vary in magnitude across color space with increasing retinal eccentricity. These shifts are not necessarily of constant magnitude, as this is strongly dependent on the color space employed. The two color opponent systems are known to differ in terms of their linearity and contrast gain.⁴⁶ We therefore do not wish to speculate about the significance of the relative magnitude of these hue shifts. However, on a qualitative level they can be simply described as shifts toward blue (in the case of pink, purple, and cyan) or toward yellow (in the case of green and orange). Previous studies have noted a similar bias toward blue and yellow in the peripheral retina^{11,24,27,29,47–50} and have attributed the shift to a number of possible causes, such as changes in the weightings of cone inputs¹⁰ and increasing rod influence,²⁹ for example. Regardless of the basis of these hue shifts, they appear to indicate a shift in the relative predominance of the blue–yellow over the red–green op-

Table 1. *t*-Statistics for the Comparisons Shown in Fig. 7

<i>t</i> -Statistics	Unique Hue versus Zero Crossing ^a				Nonunique Hue versus Hue Shift Maxima ^b			
	Red	Blue	Green	Yellow	R/B	B/G	G/Y	Y/R
<i>t</i>	-2.236	1.227	-10.161	0.580	1.595	-5.304	-3.779	0.124
df	8	8	8	8	8	8	8	8
<i>p</i>	0.056	0.255	0.000	0.578	0.149	0.001	0.005	0.904

^aComparisons between the hues identified as unique in the color naming experiments and those that exhibited zero shifts in hue with eccentricity in the asymmetric color matching experiments.

^bComparisons between the nonunique hues and those that exhibited the largest shifts in color appearance with retinal eccentricity.

ponent system in the peripheral retina. This notion has both anatomical and psychophysical support. For example, S-cone density, while variable in the central 7° – 10° of the fovea, is relatively constant beyond this eccentricity.^{51,52} This is in marked contrast to L- and M-cone densities, which steadily decrease from the fovea.⁵² These anatomical differences would appear to have functional correlates, which reveal that color vision mediated by the L–M-cone opponent system is more susceptible to compromise with increasing retinal eccentricity than that mediated by the S-cone opponent system. For example, spectral sensitivity for short wavelengths is greater in the retinal periphery.⁵³ Mullen and co-workers have found that there is a steeper decline in contrast sensitivity in the L–M- than in the S-cone opponent system.^{18,19} In addition, Vakrou *et al.*²⁰ have demonstrated that the L–M system has a greater dependency on size, which allows the maintenance of sensitivity across the retina, in comparison with the S-cone system. Taken together, all of this evidence supports the notion that color vision mediated by the L–M system possesses a greater degree of foveal specialization and becomes less prominent in the retinal periphery,^{18,19,54} where the S-cone opponent system becomes relatively more influential. This central/peripheral functional dichotomy between the two main color opponent mechanisms is consistent with the tendency toward either blue or yellow shifts in the retinal periphery and the changes in saturation,⁴⁴ and, moreover, it would seem to be a further reflection of their different genetic, anatomical, and evolutionary origins.^{55,56}

While our data show that there are systematic shifts with respect to foveal-based perception in color appearance in the peripheral retina, they indicate that these hue shifts are relatively immune to the influence of stimulus size. However, we report elsewhere that this is not so for saturation.⁴⁴ Previous studies have promoted the view that stimulus size is a particularly important factor when comparing peripheral with foveal color perception. Increasing the size of peripheral chromatic stimuli can restore many aspects of color perception to foveal levels, such as spectral sensitivity, wavelength discrimination, and hue categorization.^{6,7,32,33} However, it would appear that more subtle distortions of color perception, revealed by our color matching experiments, are still in evidence in the retinal periphery, despite the fact that the largest stimulus sizes used in this study are larger than the perceptible field sizes reported for this eccentricity for all of the color categories.⁷ This discrepancy is probably due to the fact that the perceptible field data are based on hue scaling data. As we have seen, this paradigm relies on observers' ability to rate the extent to which a color departs from red, green, blue, or yellow. As such, perhaps this paradigm is insensitive to subtle within-color category hue shifts.

B. Link with Unique Hues

Although we have failed to find an exact correspondence between all unique and nonunique hues and those hues that vary maximally and minimally with retinal eccentricity, we have, nevertheless, found a compelling degree of association between them. Unique hues can be defined

as colors that appear phenomenologically unmixed or pure⁴⁵ and are generally given the names red, green, blue, and yellow. It is well established that unique hues do not seem to be correlated with the neurophysiological properties of color opponent cells in the subcortical visual system.^{35–37,57} Their emergence as distinct sensory experiences is generally attributed to a reorganization of chromatic processing away from cone opponency at some cortical level.³⁷ Unique hues were classically defined by hue cancellation experiments,^{58,59} to which hue scaling experiments are directly relatable,⁶⁰ and they identified two perceptual or color opponent red–green and blue–yellow mechanisms based on linear inputs from L, M, and S cones with specific weighting coefficients. In such a model, unique hues occur at the equilibrium or null points of the perceptual mechanisms. Hence unique red and green occur at the equilibrium points of the blue–yellow system, while unique blue and yellow occur at the equilibrium points of the red–green system. Thus unique hues are of potential interest in studies of peripheral color vision because they represent a particular weighting of L-, M-, and S-cone inputs to color opponent mechanisms. Therefore any shift with retinal eccentricity is indicative of a change in the relative weightings of the cone inputs and represents a fundamental change in neurophysiological circuitry that underpins color perception. However, data on the invariance or otherwise of unique hues in the retinal periphery can at best be described as inconsistent. Unique yellow has been shown to be invariant,^{10,61,62} but another study reports a shift to shorter wavelengths as a function of retinal eccentricity.⁹ Unique blue, yellow, and green have been described by some as being invariant but by others as shifting to both longer and shorter wavelengths in the periphery.^{9,10,42,61,62} Unique red appears to have thus far attracted little attention, presumably because observers frequently place it in the nonspectral region of color space.

Our peripheral color matching data imply that the chromatic axes associated with the unique hue sensations are largely invariant in terms of the perceived shifts in color measured for them within the central 20° of the retina. Perhaps because we have used relatively coarse sampling of color space, we should simply state that there is minimal variation of perceived hue with eccentricity, rather than absolute invariance. Certainly it seems clear that even if the unique hues are not precisely invariant, they do not vary in hue with eccentricity to the same extent as other regions of color space. Other potential sources of discrepancies between this and previous studies might be due to the fact that the stimuli used here are more broadband in nature as opposed to the largely monochromatic stimuli that have been used previously.⁴² Furthermore, the stimuli used in this study are considerably less saturated than those used in earlier studies, and it is well-known that lines radiating out from the white point to the spectrum locus are not lines of constant hue.⁶³

The correlation between unique hues and peripherally invariant hues is weakest for unique green. Unique green has been highlighted by previous studies as exhibiting a wide variation across individual observers,⁶⁴ and some reports even suggest that unique green may have a bimodal distribution across the population,⁶⁵ although this is not

universally accepted.^{58,66} Coupled with the fact that unique green has such a large variation in the population is the finding that it is also highly dependent on experimental parameters such as chromatic adaptation and stimulus size.⁵⁸ Interestingly, Jordan and Mollon⁶⁷ noted that unique green is correlated with iris pigmentation, those subjects with lighter irides setting unique green at shorter wavelengths. This led them to speculate that unique green may not be simply genetically or physiologically determined; it seems to be strongly influenced by the external environment. Such a mechanism may be relevant to the lack of correlation between invariant and unique green found in this study.

C. Invariance as a Mechanism for Unique Hues

The association between unique hues and colors that exhibit perceptual invariance has been proposed previously in the context of the Bezold–Brücke effect.⁶⁸ This phenomenon can be observed as a perceived shift in hue with increasing intensity, and, echoing the peripheral hue shifts reported here, there are certain regions of color space that do not show the effect. Purdy,^{68,69} and later Boynton and Gordon,⁷⁰ identified three spectral regions as showing invariance with intensity, at 476, 508, and 572 nm, close to, but not exactly coincident with, unique blue, green, and yellow, respectively. Evidence suggests that the Bezold–Brücke phenomenon is different in the peripheral retina compared with the foveal region,^{71,72} particularly in terms of the nature and extent of the hue shifts. However, there appears to be little experimental evidence to indicate whether the invariant hues undergo any change with retinal eccentricity. Our prediction is that if the hues that exhibit minimal perceptual shift with retinal eccentricity and the invariant hues are indeed linked, then the latter should not shift with retinal eccentricity.

Considering the link between unique and invariant hues, Vos⁷³ concluded that although a close correspondence does exist between them, this does not necessarily mean that they have the same physiological basis. In fact it has been argued that their origins are very different. Unique hues are thought to be a function of cortical transformation of subcortical cone opponent processing, whereas invariant hue can be explained in terms of cone opponency.^{74,75} Whatever the underlying mechanism, it is interesting to speculate that unique hues might be closely related to colors that are subject to minimal distortions or shifts away from their true color appearance. These may arise from a number of sources, physiological (e.g., rod influence, cone photoreceptor nonlinearities, differing L-, M-, and S-cone input into opponent ganglion cells, changes in cone absorption, macular pigment) as well as optical (e.g., Stiles–Crawford II effects⁷⁶). Regardless of their origin, those colors that are distorted to a much lesser extent by these effects, and consequently remain constant over a larger range of stimulus parameters, have the potential to form anchor points around which color appearance systems can be organized. The corollary of this is that the least reliable, most variable colors are those that are most ambiguous to the color appearance mechanisms.

ACKNOWLEDGMENTS

We thank Janus Kulikowski and Jan Kremers for comments on earlier versions of this manuscript.

Corresponding author information: D. J. McKeefry, Department of Optometry, University of Bradford, Bradford, BD7 1DP, UK. Phone, 44 (0)1274-234648; E-mail; d.mckeefry@bradford.ac.uk.

REFERENCES

1. 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).
2. J. D. Moreland and A. Cruz, "Colour perception with the peripheral retina," *Opt. Acta* **6**, 117–151 (1959).
3. J. D. Moreland, "Peripheral colour vision," in *Visual Psychophysics*, Vol. VII/4 of Handbook of Sensory Physiology, J. Jameson and L. M. Hurvich, eds. (Springer, 1972), pp. 517–536.
4. U. Stabell and B. Stabell, "Color vision in the peripheral retina under photopic conditions," *Vision Res.* **22**, 839–844 (1982).
5. U. Stabell and B. Stabell, "Color-vision mechanisms of the extra-foveal retina," *Vision Res.* **24**, 1969–1975 (1984).
6. J. Gordon and I. Abramov, "Color vision in the peripheral retina. II. Hue and saturation," *J. Opt. Soc. Am.* **67**, 202–207 (1977).
7. 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).
8. 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).
9. H. Hibino, "Red–green and yellow–blue opponent color responses as a function of retinal eccentricity," *Vision Res.* **32**, 1955–1964 (1992).
10. J. L. Nerger, V. J. Volbrech, 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).
11. 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).
12. 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 (1993).
13. 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).
14. 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).
15. G. Wald, "Blue-blindness in the normal fovea," *J. Opt. Soc. Am.* **57**, 1289–1303 (1967).
16. D. M. Dacey, "Circuitry for color coding in the primate retina," *Proc. Natl. Acad. Sci. U.S.A.* **93**, 582–588 (1996).
17. P. R. Martin, B. B. Lee, A. J. White, S. G. Solomon, and L. Rüttger, "Chromatic sensitivity of ganglion cells in the peripheral primate retina," *Nature (London)* **410**, 933–936 (2001).
18. 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).
19. K. T. Mullen, M. Sakurai, and W. Chu, "Does L/M cone opponency disappear in the human periphery?" *Prog. Aersp. Sci.* **34**, 951–959 (2005).
20. 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).
21. N. W. Daw, R. Jensen, and W. J. Brunken, "Rod pathways in mammalian retinae," *Trends Neurosci.* **13**, 110–115 (1990).
 22. B. B. Lee, V. C. Smith, J. Pokorny, and J. Kremers, "Rod inputs to macaque ganglion cells," *Vision Res.* **37**, 2813–2828 (1997).
 23. S. Buck, "What is the hue of rod vision?" *Color Res. Appl.* **26**, S57–S59 (2001).
 24. B. Stabell and U. Stabell, "Rod and cone contributions to peripheral colour vision," *Vision Res.* **16**, 1099–1104 (1976).
 25. B. Stabell and U. Stabell, "Rod and cone contributions to change in hue with eccentricity," *Vision Res.* **19**, 1121–1125 (1979).
 26. U. Stabell and B. Stabell, "Colour vision in the peripheral retina under photopic conditions," *Vision Res.* **22**, 839–844 (1982).
 27. U. Stabell and B. Stabell, "Mechanisms of chromatic rod vision in scotopic illumination," *Vision Res.* **34**, 1019–1027 (1994).
 28. B. Stabell and U. Stabell, "Peripheral colour vision: effects of rod intrusion at different retinal eccentricities," *Vision Res.* **36**, 3407–3414 (1996).
 29. P. W. Trezona, "Rod participation in the 'blue' mechanism and its effect on colour matching," *Vision Res.* **10**, 317–332 (1970).
 30. S. Buck, R. Knight, G. Fowler, and B. Hunt, "Rod influence on hue-scaling functions," *Vision Res.* **38**, 3259–3263 (1998).
 31. R. Knight and S. L. Buck, "Time-dependent changes of rod influence on hue perception," *Vision Res.* **42**, 1651–1662 (2002).
 32. 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).
 33. 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).
 34. R. L. DeValois, I. Abramov, and G. H. Jacobs, "Analysis of response patterns of LGN cells," *J. Opt. Soc. Am.* **56**, 966–977 (1966).
 35. J. Krauskopf, D. R. Williams, and D. W. Heeley, "Cardinal directions of color space," *Vision Res.* **22**, 1123–1131 (1982).
 36. R. L. DeValois, K. K. DeValois, E. Switkes, and L. Mahon, "Hue scaling of isoluminant and cone specific lights," *Vision Res.* **37**, 885–897 (1997).
 37. R. L. DeValois, N. P. Cottaris, S. D. Elfar, L. E. Mahon, and J. A. Wilson, "Some transformations of color information from lateral geniculate nucleus to striate cortex," *Proc. Natl. Acad. Sci. U.S.A.* **97**, 4997–5002 (2000).
 38. A. Valberg, "Unique hues: an old problem for a new generation," *Vision Res.* **41**, 1645–1657 (2001).
 39. A. M. Derrington, J. Krauskopf, and P. Lennie, "Chromatic mechanisms in lateral geniculate nucleus of macaque," *J. Physiol. (London)* **357**, 241–265 (1984).
 40. M. J. Sankeralli and K. T. Mullen, "Assumptions concerning orthogonality in threshold-scaled versus cone-contrast colour spaces," *Vision Res.* **41**, 53–55 (2001).
 41. K. Knoblauch and M. D'Zmura, "Lights and neural responses do not depend on choice of colour space," *Vision Res.* **41**, 1683–1684 (2001).
 42. 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).
 43. V. C. Smith and J. Pokorny, "Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm," *Vision Res.* **15**, 161–171 (1975).
 44. D. J. McKeefry, N. R. A. Parry, and I. J. Murray, Department of Optometry, University of Bradford, UK are preparing a manuscript to be called "Perceived shifts in saturation of chromatic stimuli in the near peripheral retina."
 45. J. D. Mollon and G. Jordan, "On the nature of unique hues," in *John Dalton's Colour Vision Legacy*, C. Dickinson, I. Murray, and D. Carden, eds. (Taylor & Francis, 1997), pp. 381–392.
 46. J. Larimer, D. H. Krantz, and C. M. Cicerone, "Opponent processes additivity—II. Yellow/blue equilibria and nonlinear models," *Vision Res.* **15**, 723–731 (1975).
 47. R. Lythgoe, "Dark-adaptation and the peripheral colour sensations of normal subjects," *Br. J. Ophthalmol.* **15**, 193–210 (1931).
 48. R. W. G. Hunt, "Light and dark adaptation and the perception of color," *J. Opt. Soc. Am.* **42**, 190–199 (1952).
 49. S. Buck, "Influence of rod signals on hue perception: evidence from successive scotopic color contrast," *Vision Res.* **37**, 1295–1301 (1997).
 50. 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).
 51. D. R. Williams, D. I. R. MacLeod, and M. M. Hayhoe, "Foveal tritanopia," *Vision Res.* **21**, 1341–1356 (1981).
 52. 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).
 53. B. Stabell and U. Stabell, "Absolute spectral sensitivity at different eccentricities," *J. Opt. Soc. Am.* **71**, 836–840 (1981).
 54. K. T. Mullen, "Color vision as a post-receptoral specialization of the central visual-field," *Vision Res.* **31**, 119–130 (1991).
 55. J. D. Mollon, "Color vision," *Annu. Rev. Psychol.* **33**, 41–85 (1982).
 56. J. Nathans, D. Thomas, and D. S. Hogness, "Molecular genetics of human color vision: the genes encoding blue, green, and red pigments," *Science* **232**, 193–202 (1986).
 57. I. Abramov and J. Gordon, "Color appearance: on seeing red—or yellow, or green, or blue," *Annu. Rev. Psychol.* **45**, 451–485 (1994).
 58. L. M. Hurvich, D. Jameson, and J. D. Cohen, "The experimental determination of unique green in the spectrum," *Percept. Psychophys.* **4**, 65–68 (1968).
 59. R. M. Boynton, "Color, hue and wavelength," in *Handbook of Perception*, E. C. Carterette and M. P. Freidman, eds. (Academic, 1975), Vol. 8.
 60. J. Gordon and I. Abramov, "Scaling procedures for specifying color appearance," *Color Res. Appl.* **13**, 146–152 (1988).
 61. J. L. Nerger, V. J. Volbrecht, C. J. Ayde, and S. M. Imho, "Effect of the S-cone mosaic and rods on red/green equilibria," *J. Opt. Soc. Am. A* **15**, 2816–2826 (1998).
 62. I. Abramov and J. Gordon, "Seeing unique hues," *J. Opt. Soc. Am. A* **22**, 2143–2153 (2005).
 63. S. M. Newhall, D. Nickerson, and D. B. Judd, "Final report of the OSA subcommittee on the spacing of Munsell colours," *J. Opt. Soc. Am.* **33**, 385–412 (1943).
 64. W. Richards, "Differences among colour normals: classes I and II," *J. Opt. Soc. Am.* **57**, 1047–1055 (1967).
 65. M. L. Rubin, "Spectral hue loci of normal and anomalous trichromats," *Am. J. Ophthalmol.* **52**, 166–172 (1961).
 66. V. J. Volbrecht, J. L. Nerger, and C. E. Harlow, "The bimodality of unique green revisited," *Vision Res.* **37**, 407–416 (1997).
 67. G. Jordan and J. D. Mollon, "Rayleigh matches and unique green," *Vision Res.* **35**, 613–620 (1995).
 68. D. Purdy, "The Bezold–Brücke phenomenon and contours for constant hue," *Am. J. Psychol.* **49**, 313–315 (1937).
 69. D. Purdy, "Spectral hue as a function of intensity," *Am. J. Psychol.* **43**, 541–559 (1931).
 70. R. Boynton and J. Gordon, "Bezold–Brücke hue shift measured by color-naming technique," *J. Opt. Soc. Am.* **55**, 78–86 (1965).
 71. B. Stabell and U. Stabell, "Bezold–Brücke phenomenon of

- the far peripheral retina," *Vision Res.* **22**, 845–849 (1982).
72. S. M. Imhoff, V. J. Volbrecht, and J. L. Nerger, "A new look at the Bezold–Brücke hue shift in the peripheral retina," *Vision Res.* **44**, 1–16 (2004).
73. J. J. Vos, "Are unique and invariant hues coupled?" *Vision Res.* **26**, 337–342 (1986).
74. D. B. Judd, "Response functions for types of vision according to the Muller theory," *J. Res. Natl. Bur. Stand.* **42**, 1–16 (1949).
75. C. R. Ingling and B. Tsou, "Orthogonal combinations of the three visual channels," *Vision Res.* **17**, 1075–1082 (1977).
76. J. M. Enoch and W. S. Stiles, "The colour change of monochromatic light with retinal angle of incidence," *Opt. Acta* **8**, 329–358 (1961).