

# Measurements of Chromatic Sensitivity in the Mesopic Range

Helen C. Walkey,<sup>1\*</sup> John L. Barbur,<sup>1</sup>  
J. Alister Harlow,<sup>1</sup> Walter Makous<sup>2</sup>

<sup>1</sup> Applied Vision Research Centre, City University, 311-321 Goswell Road, London, EC1V, 7DD, UK

<sup>2</sup> Center for Visual Science, University of Rochester, Rochester, NY

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*Abstract:* We measured chromatic threshold sensitivity in the mesopic range using a combination of techniques that mask the detection of photopic and scotopic luminance contrast signals. The measurements were carried out at a number of light levels in the range 45–0.004 cd/m<sup>2</sup>, both foveally and with the stimulus centered 3.5° in the periphery. In order to investigate the effect of rod signals on chromatic detection thresholds in the near periphery of the visual field, we measured chromatic threshold ellipses when fully dark-adapted and during the cone plateau region of the dark-adaptation curve. The results confirm a number of previous observations and reveal new findings:

- A reduction in background adaptation causes a loss of chromatic sensitivity that becomes more rapid as one enters the mesopic range. This loss is observed both foveally and in the near periphery and cannot, therefore, be attributed entirely to rod intrusion. A small increase in chromatic thresholds is observed in the near periphery when compared with foveal measurements. Comparison of foveal and peripheral measurements also reveals a tilt in the orientation of the major axis of the chromatic threshold ellipse away from the tritanopic towards the deuteranopic colour confusion line:
- The loss of chromatic sensitivity is not uniform, with the tritan axis being most affected. The ellipticity (i.e., the ratio of major to minor axis of the ellipse plotted on the CIE 1976, UCS diagram) can increase by as much as a

factor of two, as the light level decreases from 10–0.056 cd/m<sup>2</sup>.

- At lower light levels, some subjects show an asymmetry in chromatic thresholds along the tritan axis. This asymmetry is consistent with greater sensitivity to increases than decreases in S-cone excitation.
- Measurements of chromatic sensitivity following either complete dark-adaptation or during the cone plateau phase of the dark-adaptation curve yield essentially the same results. These findings, therefore, suggest that rod signals have little or no influence on chromatic sensitivity at this eccentricity. © 2000 John Wiley & Sons, Inc. *Col Res Appl*, 26, S36–S42, 2001

*Key words:* colour vision; chromatic sensitivity; mesopic vision; dark adaptation; rod-cone interaction

## INTRODUCTION

Mesopic vision describes a range of light levels, where vision is mediated by both rods and cones. The relative contribution to visual perception made by rods and cones in this range varies with the level of light adaptation and other parameters such as stimulus size, spectral content, eccentricity, and duration of presentation. This region spans a range of light levels, which extends from 5000 scotopic trolands, just below rod saturation,<sup>1</sup> to almost absolute threshold, depending on background and stimulus conditions. The mesopic range, therefore, encompasses lighting conditions from, for example, twilight, night driving, and emergency lighting levels to about the luminance of blue sky.<sup>2</sup> Even at the lowest end of this range, colour vision can contribute significantly to the visual response.<sup>3,4</sup>

Although colour vision does extend to these low levels, chromatic sensitivity deteriorates significantly at luminances below about 3 cd/m<sup>2</sup>, with normal observers becoming tritanomalous at mesopic levels.<sup>5,6</sup> Normal subjects

\* Correspondence to: Helen C. Walkey, City University, Applied Vision Research Centre, Northampton Square, London EC1V 0HB, UK (e-mail: h.c.walkey@city.ac.uk)

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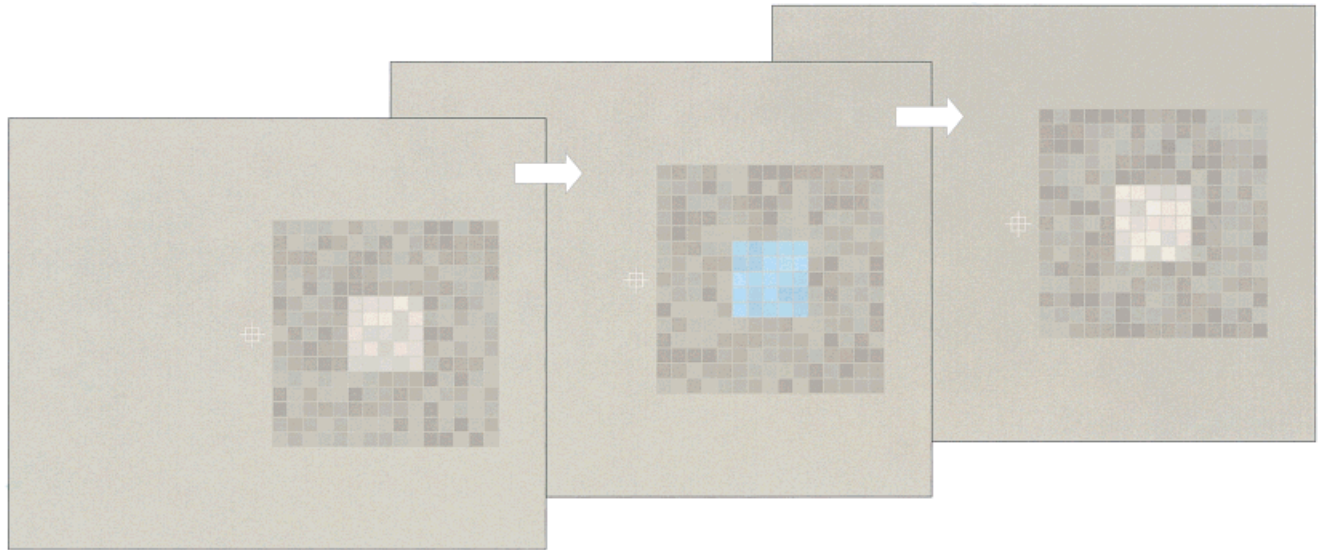


FIG. 1. Example of visual stimuli designed to isolate the use of chromatic signals. The spatial luminance distribution of the checks and the mean luminance of the central square changes randomly every 107 ms, generating dynamic luminance contrast noise and light flux noise, respectively. Each presentation lasts 1.5 s, with the coloured stimulus presented for 0.5 s in the middle of this range. (See Methods for full details.)

show increased tritan errors on the FM-100 Hue test performed under low illumination.<sup>7-10</sup> Reduction of retinal illuminance also produces a deterioration of wavelength discrimination over much of the visual spectrum with, in particular, greatly reduced discrimination over the mid-wavelength region of the spectrum. However, an improvement in discrimination can be seen at roughly 460 nm,<sup>11</sup> especially when short flash durations are involved.<sup>12</sup> There is little doubt that, in general, colour vision deteriorates at low light levels and this can be quantified by measurements of perceived chromatic saturation, wavelength discrimination, and colour detection thresholds. This observed degradation in visual performance has been attributed largely to lower signal-to-noise ratios in cone receptors at low light levels, and the effect rod signals may have on chromatic pathways.<sup>13</sup> It is, however, by no means clear how the contribution of these factors changes with light adaptation level and other stimulus conditions.

Previous studies of chromatic discrimination have involved either direct measurement of the just noticeable difference between two coloured fields, or an estimate of standard deviation derived from a number of colour matches made between a fixed and variable field. Both methods require setting isoluminance for the fixed and the variable field, which is often difficult to carry out. In this study, we have investigated the loss of chromatic sensitivity in the mesopic range using a dynamic luminance perturbation technique that isolates the use of chromatic signals. The advantage of this technique is that it eliminates the need to determine isoluminance. Our metric for chromatic sensitivity also differed from previous studies; we measured the threshold for detection of a chromaticity change against a neutral background. Of interest was also the need to examine further the preferential loss of blue-yellow sensitivity at low light levels, which has been reported in the literature, in

particular, the extent to which this loss can be attributed to rod involvement or selective reduction of the signal-to-noise ratio in cone receptors.

## METHODS

To isolate chromatic signals in the mesopic range, we designed a masking technique to eliminate the detection of photopic and scotopic luminance contrast signals associated with a chromatic change. The colour vision test used in this study simultaneously employed three types of luminance contrast masking: luminance contrast noise (LC), large-field light flux noise (LF), and the presence of a luminance contrast pedestal (LCP). The stimulus for the test field consisted of an array of checks, the central square of which was defined by an LCP and formed the test target (see Fig. 1). LC masking was provided by randomly modulating the luminance of each check in the array within a range specified as a percentage of the stimulus luminance. The duration of each frame was 107 ms, and the mean luminance of the stimulus remained constant. LF masking was provided by the random modulation of the mean luminance of the test target and was independent of ongoing LC noise. The benefit of using local, dynamic LC noise to mask photopic contrast signals has been demonstrated successfully in both normal trichromats and dichromats,<sup>14</sup> and in patients with cerebral achromatopsia.<sup>15</sup> In a similar way, LF noise was designed to mask spatially pooled rod signals that cannot be masked with LC noise.<sup>16</sup> The use of a luminance contrast-defined pedestal helps further to mask the detection of luminance contrast changes at the onset of a chromatic stimulus.<sup>17</sup>

Stimuli were presented on a CRT monitor (Sony Multi-scan 20"), which was calibrated for the luminance vs. gun

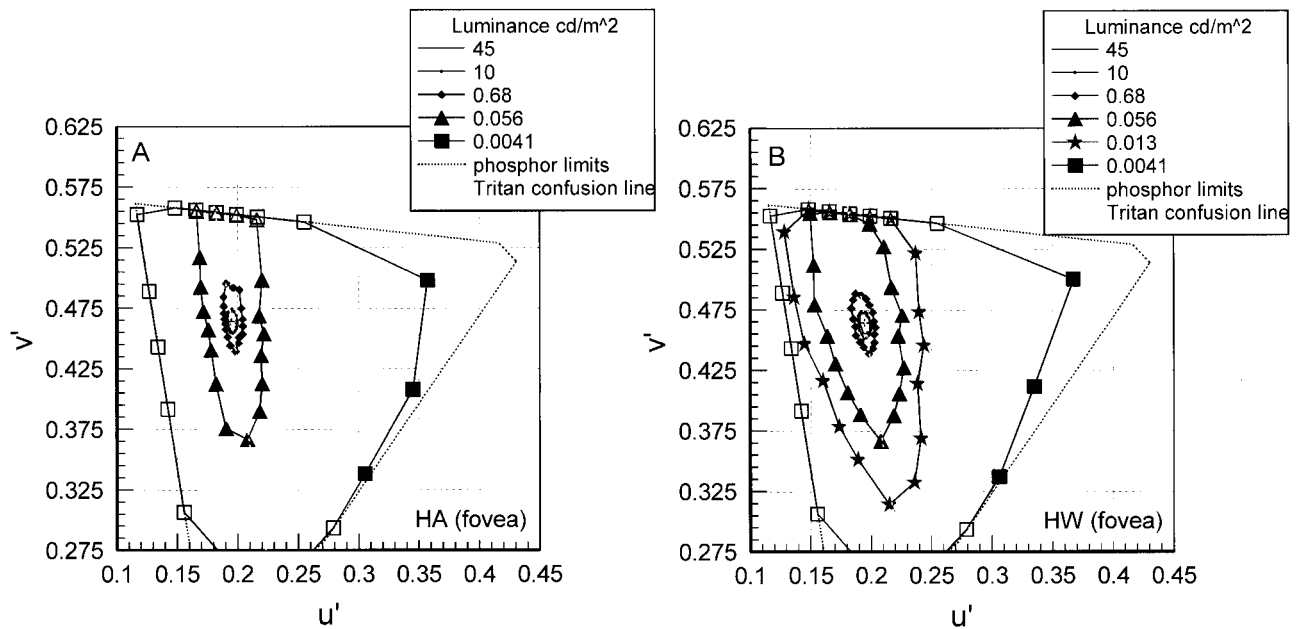


FIG. 2. (A)–(B) Chromatic threshold ellipses for two subjects measured foveally for each of the light levels investigated: (section A) HW and (section B) HA. The closed symbols indicate chromatic thresholds. The open symbols indicate that threshold was not attained before reaching the limits imposed by the phosphors of the display and an arbitrary maximum value has been assigned (the maximum saturation that can be produced by the display).

voltage relationship for each of the three guns using a LMT (L1003) photometer. The three display phosphors were also calibrated for radiance and chromaticity using a Gamma Scientific telespectroradiometer (model RD2). Standard colorimetric transformations<sup>18</sup> were then used to compute the phosphor luminances required to generate a specified luminance/chromaticity triplet. Spectrally calibrated neutral density filters were employed to achieve a 4-log unit change in mean luminance level.

A psychophysical staircase procedure was used to measure thresholds for detection of chromatic changes. Measurements were obtained for a 2.0° square stimulus presented on a uniform background of angular subtense 29° × 23° (Fig. 1). A single stimulus lasted 1500 ms; the change of chromaticity lasted only for 500 ms and was arranged to be in the middle of each presentation. Each stimulus represented a shift in the chromaticity of the test target, away from background chromaticity towards the spectrum locus, in one of 18 directions. Chromatic saturation in each direction was measured in the CIE 1931 ( $x, y$ )-chromaticity space and controlled by one of 18 randomly interleaved staircases. The values derived from each staircase correspond to the chromatic threshold in each direction investigated. The data points determined in the CIE 1931 ( $x, y$ )-chromaticity space were then transformed to the CIE 1976 ( $u', v'$ )-chromaticity space and plotted in this space. No attempt was made to fit elliptical functions to the data.

Four colour normal observers (age range 22–47) took part in this study. All observations were made monocularly with the right eye and with natural pupils. Two subjects: HA and HW carried out measurements for five light levels in the range 45–0.0041 cd/m<sup>2</sup>, following appropriate dark-adaptation. The stimulus was centered either at the fovea, or 3.5°

from fixation in the right hemifield. An eccentricity of 3.5° was chosen, because in the near periphery it is relatively easy to carry out the measurements, and also because it corresponds to a retinal location where rods are present. The neutral background chromaticity was  $u' = 0.195, v' = 0.464$ , corresponding to “MacAdam white.”<sup>19</sup> When testing at the higher light levels, random luminance masking was set at ±20% of the mean luminance of the stimulus. For the lower light levels and more peripheral measurements, this value was increased to ±40% to compensate for the large increase in luminance contrast thresholds.

Three subjects: HW, JB, and SM carried out measurements at a single light level following dark-adaptation and also on the cone plateau of the dark-adaptation curve. For this experiment, the chromaticity of the background was  $u' = 0.198, v' = 0.395$ , and the stimulus was positioned at 3.5° eccentricity. A Maxwellian view optical system<sup>20</sup> was used to generate a white-light bleaching stimulus (of correlated colour temperature 3200 K). The stimulus field was circular, of 48° diameter and retinal illuminance 5-log trolands. The subject was light-adapted for 2 min and preliminary dark-adaptation measurements were used to establish the duration of the cone plateau following bleaching. Measurements started 4 min after the end of the bleach and continued for 4 min and 30 s, and then the bleach was repeated. The measurement of one complete chromatic threshold ellipse required 3–4 bleaches.

## RESULTS

### Foveal Measurements

Figure 2 shows foveal chromatic threshold ellipses measured in two subjects for each of the five light levels

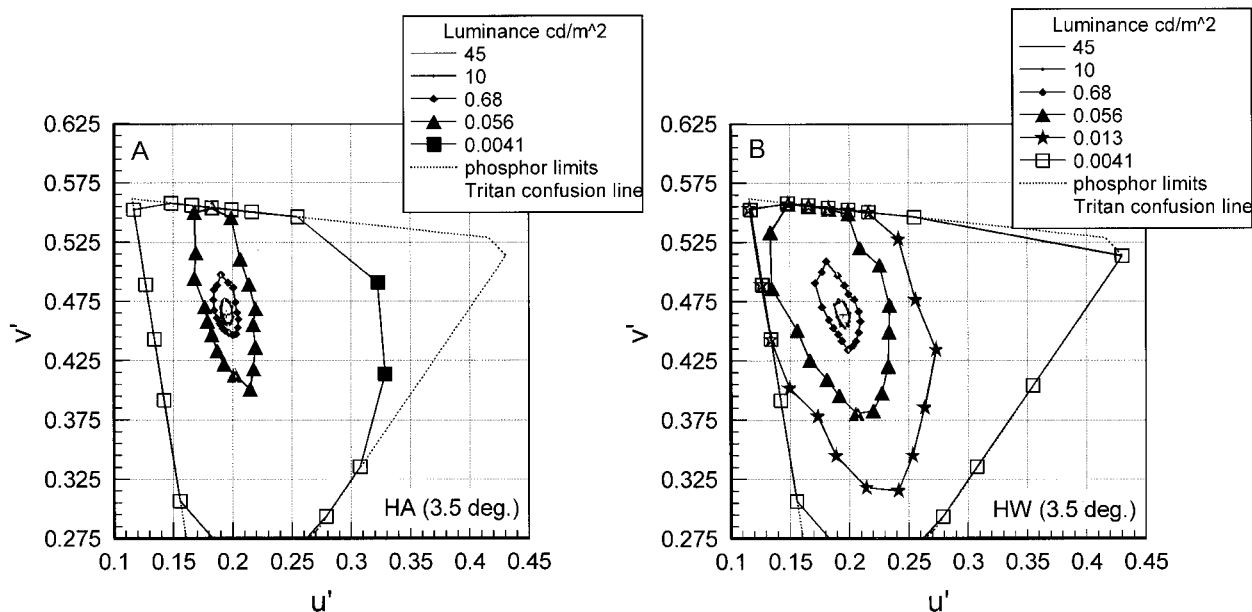


FIG. 3. (A)–(B) Chromatic threshold ellipses measured for each of the light levels investigated with the stimulus centered 3.5° in the periphery: (section A) HW and (section B) HA. The closed symbols indicate chromatic thresholds. The open symbols indicate that threshold was not attained before reaching the limits imposed by the phosphors of the display and an arbitrary maximum value has been assigned (the maximum saturation that can be produced by the display).

investigated (measurements were obtained at an additional light level: 0.013 cd/m<sup>2</sup> for subject HW). The results are plotted in the CIE 1976 ( $u'$ ,  $v'$ )-uniform chromaticity space. The data points represent the mean of three separate measurements. When testing at the lower light levels (0.056, 0.013, and 0.0041 cd/m<sup>2</sup>), it was not possible to measure thresholds in all directions, because we were constrained by the limits of the phosphors of the display. In such cases, the maximum achievable chromatic saturation was plotted. These points coincide with the curve that plots the phosphor limits in Fig. 2. For the lowest light level tested (0.0041 cd/m<sup>2</sup>), thresholds could be measured for only a few of the 18 directions.

The measured thresholds show only small differences when the light level changes from 45 and 10 cd/m<sup>2</sup>. However, at lower light levels, thresholds are elevated, and the different colour directions become perceptually less separable and more difficult to distinguish on the basis of colour appearance. Nevertheless, all subjects were aware of colour changes, and when questioned could label correctly the principal hues. The major axes of these ellipses are aligned with the tritan colour confusion line.<sup>21</sup> As luminance decreases, the ellipses of observer HA elongate along this axis, leading to a doubling of ellipticity (ratio major to minor axis) over the range of light levels tested, but observer HW shows little elongation with decreased luminance. At the lower light levels, however, we were not able to estimate the actual ellipticity, because the limits imposed by the phosphors of the display obscure the ellipse boundaries. This leads to underestimation of the actual increase in ellipticity.

### Peripheral Measurements

Figure 3 shows thresholds obtained with the stimulus centered 3.5° in the periphery. The results show a gradual loss of sensitivity with increased ellipticity at lower light levels. The major axes of these ellipses show a slight deviation from the tritanopic confusion line towards a red-green axis. We have also observed this effect in other unpublished studies when the subjects become deutan-like at large eccentricities.

### Change of Background Chromaticity

The ellipses measured at 45 and 10 cd/m<sup>2</sup> both at the fovea and in the near periphery show symmetry with respect to background chromaticity. The symmetry present at the lower mesopic levels studied, i.e., 0.056 and 0.013 cd/m<sup>2</sup>, is difficult to evaluate because of the aforementioned masking of the ellipse boundaries. To overcome the constraints set by these limits and further investigate the possible symmetry of such ellipses, we repeated a set of measurements at 0.056 cd/m<sup>2</sup> and 3.5° eccentricity, but with a change of background chromaticity. Figure 4 shows the results obtained for subject HW, when the neutral background was shifted from  $u' = 0.195$ ,  $v' = 0.464$  to  $u' = 0.198$ ,  $v' = 0.395$ . At this chromaticity, the background appeared bluish gray. With the new background chromaticity, it was possible to obtain threshold measurements in all 18 directions; revealing, for this subject, an ellipse that is asymmetric about the background along the blue-yellow axis. The asymmetry corresponds to a reduced sensitivity for S-cone decrements (i.e.,

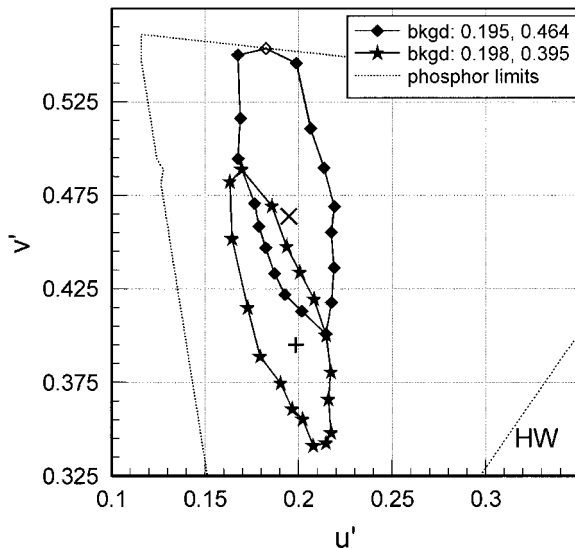


FIG. 4. Chromatic threshold ellipses measured  $3.5^\circ$  in the periphery, at a luminance of  $0.056 \text{ cd/m}^2$  for two backgrounds of different chromaticity. The first background chromaticity corresponds approximately to daylight at a colour temperature of  $6500 \text{ K}$ . The second results in a more bluish-gray appearance and was selected to allow greater changes of chromaticity for all colour directions investigated. The closed symbols indicate chromatic thresholds. The open symbols indicate that threshold was not attained before reaching the limits imposed by the phosphors of the display, and an arbitrary maximum value has been assigned (the maximum saturation that can be produced by the display).

the yellow direction), and/or an increased sensitivity for S-cone increments (i.e., the blue direction).

### Cone Plateau Measurements

The asymmetry found for ellipses measured at the lower light levels, which is not as evident at high light levels, suggests that the effect may be produced by the influence of rod signals on chromatic processes. To test this hypothesis, we compared thresholds following complete dark-adaptation to a given background luminance, with those measured

on the cone plateau of the dark-adaptation curve for the same background luminance. The stimulus was centred  $3.5^\circ$  in the periphery at an eccentricity, where rods should contribute to the response. The lowest pedestal light level that we were able to employ for testing on the cone plateau was  $0.09 \text{ cd/m}^2$ . These results are shown in Fig. 5. Under these conditions, threshold contours vary somewhat between observers. However, none of the three observers showed significant changes in the thresholds obtained after dark-adaptation relative to those obtained on the cone plateau. Subject HW exhibits marginally larger thresholds than either JB or SM, and shows the aforementioned asymmetry along the blue-yellow axis [Fig. 5(C)]. Subject SM shows qualitatively the same asymmetry, but subject JB shows no asymmetry.

### DISCUSSION

The results of this investigation confirm a number of previous observations, and reveal some new findings. It is clearly well established that the lowering of background light adaptation causes an overall reduction in chromatic sensitivity. This can be demonstrated in wavelength discrimination experiments<sup>11</sup> or chromatic discrimination measurements.<sup>5</sup> The results reported here show that the loss of chromatic sensitivity in the mesopic range is observed both foveally and with the stimulus centered  $3.5^\circ$  in the periphery. Rod intrusion cannot, therefore, entirely explain these findings. It is also known that the use of dynamic LC noise fails to cause any significant increase in chromatic detection thresholds in the photopic range.<sup>15,22</sup> The results of this study suggest that chromatic and luminance contrast signals are also processed separately in the mesopic range.

An interesting observation concerns the use of the CIE 1976 ( $u'$ ,  $v'$ )-uniform chromaticity space. This system was introduced to correct for the nonuniformity in the CIE 1931 chromaticity diagram. Figure 2 shows that even at moderate levels of light adaptation the measured thresholds are not independent of the direction tested. Instead of forming circles, the threshold contours describe ellipses with their

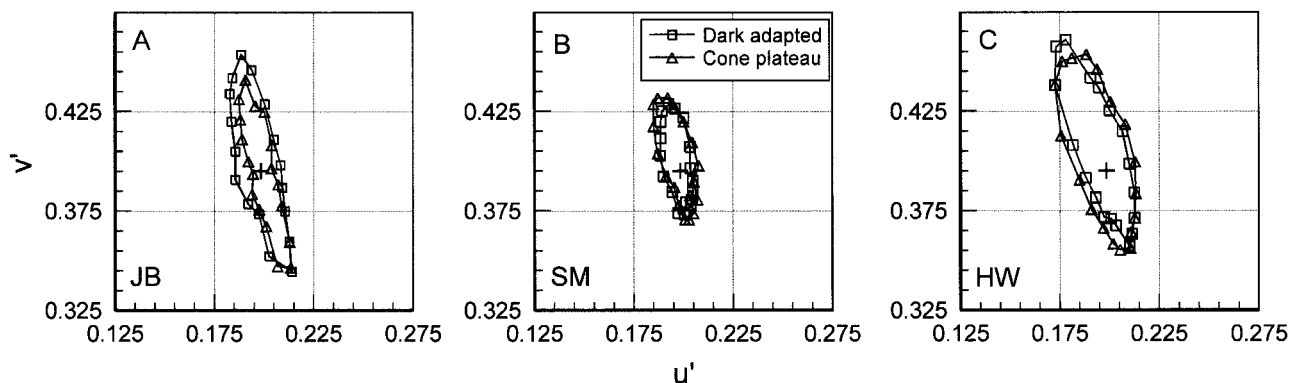


FIG. 5. (A)–(C) Comparison of dark-adapted and cone-plateau thresholds. The results shown were measured with the stimulus centered  $3.5^\circ$  in the periphery at a luminance of  $0.09 \text{ cd/m}^2$ , following (squares) dark adaptation and on the cone plateau of (triangles) the dark adaptation curve: (section A) subject JB, (section B) subject SM, and (section C) HW.

major axis aligned with the blue-yellow axis, as determined by the tritan confusion line. As luminance decreases, the nonuniformity becomes more pronounced; the ellipses elongate along this axis, often leading to a doubling of ellipticity. The nonuniformity of the  $u'$ ,  $v'$  space is well known, but it does complicate inferences about the ellipticity of the locus of chromatic difference thresholds and their asymmetry, especially inferences about their magnitude. However, *changes* in the ellipticity or asymmetry with luminance or other variables cannot be attributed to nonuniformity of the colour space employed.

The nonuniform elevation of chromatic thresholds produced by the reduction of retinal illuminance is consistent with the findings of Brown.<sup>5</sup> The selective loss of chromatic sensitivity, along the blue-yellow axis is also consistent with the finding of tritan errors for the FM-100 Hue test, when performed under low illumination.<sup>7–10</sup>

Closer examination of thresholds along the blue-yellow axis at low light levels raises the question of whether rod influences on chromatic mechanisms either contribute to the observed increase in thresholds or cause the threshold asymmetry along a tritan axis. Figure 5 shows a comparison of chromatic thresholds measured  $3.5^\circ$  in the periphery, on the cone plateau region of the dark-adaptation curve, where rod influences should be absent, and after full dark adaptation to the same background level, where rod influences should be maximal. The absence of significant differences between the two sets of data suggests that neither the selective loss of chromatic sensitivity along the tritan axis nor the asymmetry in thresholds in the blue and yellow directions can be attributed to rod signals. This may not, however, be the case for other stimulus conditions. There is evidence that both red-green discrimination at  $25^\circ$  eccentricity<sup>23</sup> and yellow-blue discrimination at  $7^\circ$  eccentricity<sup>24</sup> in the mesopic range are impaired by the influence of rods. Wavelength discrimination at  $7^\circ$  eccentricity also appears to be impaired by rod intrusion, but not at  $2.5^\circ$ .<sup>25</sup> We suggest, therefore, that rod influences may not impair chromatic discrimination in the near periphery of the visual field (e.g.,  $< 3.5^\circ$ ). The reported impairment of tritan scores on the FM-100 hue test,<sup>10</sup> where presumably foveal viewing was also used, is entirely consistent with a selective loss of chromatic sensitivity along the tritan axis at low light levels. The authors find that error scores along the tritan axis increase systematically as the light level decreases and this is consistent with the results of this study (see Figs. 2–4). When the FM-100 Hue test is carried out during the cone-plateau condition, the errors reduce significantly, and the authors interpret this observation as evidence for involvement of rod signals. That experiment and the one carried out here are, however, different, in that caps that form the FM-100 hue test were viewed against a dark background, whereas the test stimulus in our study is a luminance pedestal presented against a background field (see Fig. 1). This and other differences between the two tests may explain why we do not find a difference in thresholds between the dark-adapted and cone-plateau conditions.

The general reduction of chromatic sensitivity in the

mesopic range can be explained by the reduction in quantal catch of the cone receptors and a corresponding decrease in signal-to-noise ratio. The preferential loss of blue-yellow sensitivity observed at low light levels could be due to either the scarcity of S-cones in the retina,<sup>26</sup> or due to S-cone signals only operating in the Weber region for higher levels of S-cone excitation.<sup>27,28</sup> This explanation can also account for the observed asymmetry in chromatic sensitivity that is present in some subjects [see Fig. 5(B)–(C)]. If S-cones operate just outside the Weber region at lower light levels, detection thresholds are larger in the yellow direction, where the S-cone signals decrease and, therefore, move further away from the Weber region. Similarly, detection thresholds are smaller in the blue direction, where S-cone signals increase and move more into the Weber region. This kind of behavior predicts an improvement in sensitivity towards the blue and an impairment of sensitivity towards the yellow. This hypothesis also predicts that changes in background adaptation level should either enhance or reduce the observed asymmetry in chromatic thresholds when S-cones are involved. DeMarco *et al.*<sup>29</sup> observed symmetry in such thresholds at  $\approx 100 \text{ cd/m}^2$ , and Shinomori *et al.*<sup>30</sup> observed equal sensitivity to both directions of sawtooth temporal modulation of S-cone excitation at  $3 \text{ cd/m}^{-2}$ , although they were able to produce differences by adaptation to such asymmetrical stimuli. The asymmetry in the thresholds for increments and decrements of S-cone excitation is observed in only some subjects and appears to depend on luminance, state of adaptation, and probably other factors. More experimental work is, therefore, needed to test this hypothesis and to explain why the chromatic threshold asymmetry along the tritan axis is not present in all subjects.

#### ACKNOWLEDGMENTS

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1. Aguilar M, Stiles WS. Saturation of the rod mechanism of the retina at high levels of illumination. *Optica Acta* 1954;1:59–65.
2. Makous W. Optics. In: Carpenter RHS, Robson JG, editors. *Vision research: a practical guide to laboratory methods*. Oxford: Oxford University Press; 1998. p 1–49.
3. Stabell B, Stabell U. Absolute spectral sensitivity at different eccentricities. *J Opt Soc Am* 1981;71:836–840.
4. Barbur JL, Harlow AJ, Smith P, Hurden A. Visual performance in the mesopic range. In: *Non-invasive assessment of the visual system. Volume 1 (Technical Digest Series)*. Washington DC: Optical Society of America; 1998. p 140–143.
5. Brown WR. The influence of luminance level on visual sensitivity to color differences. *J Opt Soc Am* 1951;41:684–688.
6. Lorbeer B, Rentschler I, Rohler R. Pseudo-tritan effect and the Vos–Walraven line element at low luminance levels. *Vision Res* 1976;16: 221–223.
7. Bowman KJ, Cole BL. A recommendation for the illumination of the Farnsworth–Munsell 100-hue test. *Am J Optomol Phys Opt* 1980;57: 839–843.
8. Knoblauch K, Saunders F, Kusuda M, Hynes R, Podgor M, Higgins

- KE, de Monasterio FM. Age and illuminance effects in the Farnsworth–Munsell 100-hue test. *Appl Opt* 1987;26:1441–1448.
9. Smith VC, van Everdingen J, Pokorny J. Sensitivity of arrangement tests as evaluated in normals at reduced levels of illumination. In: Drum B, Moreland JD, Serra A, editors. *Doc Ophthalmol Proc Ser, Colour Vision Deficiencies X*. Dordrecht: Kluwer; 1991. p 177–185.
  10. Knight R, Buck SL, Fowler GA, Nguyen A. Rods affect S-cone discrimination on the Farnsworth–Munsell 100-hue test. *Vision Res* 1998;38:3477–3481.
  11. McCree KJ. Small-field tritanopia and the effects of voluntary fixation. *Optica Acta* 1960;7:317–323.
  12. Mollon JD, Astell S, Cavonius CR. A reduction in stimulus duration can improve wavelength discriminations mediated by short-wave cones. *Vision Res* 1992;32:745–755.
  13. Trezona PW. Rod participation in the ‘blue’ mechanism and its effect on colour matching. *Vision Res* 1970;10:317–332.
  14. Birch J, Barbur JL, Harlow AJ. A new method based on random luminance masking for measuring isochromatic zones using high resolution colour displays. *Ophthalmic & Physiol Opt* 1992;12:133–136.
  15. Barbur JL, Harlow JA, Plant GT. Insights into the different exploits of colour in the visual cortex. *Proc Roy Soc Lond B* 1994;258:327–334.
  16. Cole VA, Barbur JL, Harlow AJ. Pupil light reflex components isolated using contrast and light flux masking techniques. *Investigat Ophthalmol Visual Sci* 1995;36:940.
  17. Brown WR, MacAdam DL. Visual sensitivities to combined chromaticity and luminance differences. *J Opt Soc Am* 1949;39:808–834.
  18. Wyszecki GW, Stiles WS. *Color science — Concepts and methods, quantitative data and formulae*. 2<sup>nd</sup> ed. New York: Wiley; 1982. 950 p.
  19. MacAdam DL. Visual sensitivities to color differences in daylight. *J Opt Soc Am* 1942;32:247–274.
  20. Barbur JL, Ruddock KH. Spatial characteristics of movement detection mechanisms in human vision I: achromatic vision. *Biol Cybern* 1980;37:77–92.
  21. Nakano Y. Color vision mathematics: A tutorial. In: Kaiser PK, Boynton RM. *Human color vision*. 2<sup>nd</sup> ed. Washington DC: Optical Society of America; 1996. p 545–562 (Appendix, part III).
  22. Mullen KT, Cropper SJ, Losada MA. Absence of linear subthreshold summation between red-green and luminance mechanisms over a wide range of spatio-temporal conditions. *Vision Res* 1997;37:1157–1165.
  23. Nagy AL, Doyal JD. Red-green color discrimination as a function of a stimulus field size in peripheral vision. *J Opt Soc Am* 1993;10:1147–1156.
  24. Knight R, Buck SL, Pereverzeva M. Stimulus size affects rod influence on Tritan Chromatic Discrimination. *Col Res Appl Suppl* 2001;26: S65–S68.
  25. Stabell U, Stabell B. Wavelength discrimination of peripheral cones and its change with rod intrusion. *Vision Res* 1977;17:423–426.
  26. Curcio CA, Allen KA, Sloan KR, Lerea CL, Hurley JB, Klock IB, Milam AH. Distribution and morphology of human cone photoreceptors stained with blue anti-blue opsin. *J Compar Neurol* 1991;312: 610–624.
  27. Boynton RM, Kambe N. Chromatic difference steps of moderate size measured along theoretically critical axes. *Col Res Appl* 1980;5:13–23.
  28. Yeh T, Pokorny J, Smith VC. S-cone discrimination sensitivity and performance on arrangement tests. In: Drum B, editor. *Doc Ophthalmol Proc Ser, Colour Vision Deficiencies XI*. Dordrecht: Kluwer; 1993. p 293–302.
  29. DeMarco PJ, Smith VC, Pokorny J. Effect of sawtooth polarity on chromatic and luminance detection. *Visual Neurosci* 1994;11:491–499.
  30. Shinomori K, Spillmann L, Werner JS. S-cone signals to temporal OFF-channels: asymmetrical connections to postreceptoral chromatic mechanisms. *Vision Res* 1999;39:39–49.