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The Ratio of L Cones to M Cones in the Human Parafoveal Retina*

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We present psychophysically-based estimates of the relative numbers of long-wavelength-sensitive (L) and middle-wavelength-sensitive (M) cones in the parafovea of three color-normal trichromats. Using methods previously applied to the fovea centralis, we obtained estimates of the relative numbers of L and M cones at retinal eccentricities of 1.0, 1.5, 2.0, 3.0, and 4.0 deg along the horizontal meridian of the temporal retina. Results for three observers indicate that the L to M cone ratio remains approximately invariant from the fovea to 4.0 deg eccentricity, with a mean ratio near 2:1.

Cones Human parafovea Ratio of L to M cones

INTRODUCTION

In the human retina, changes with eccentricity in the distribution, size, and organization of the rods and cones are known primarily from the classic work of Østerberg (1935) and more recent histological studies of Curcio, Sloan, Packer, Hendrickson and Kalina (1987), Ahnelt, Kolb and Pflug (1987), and Curcio, Sloan, Kalina and Hendrickson (1990). Although changes in the density of the total number of cones with eccentricity are known from these studies, changes for the separate subpopulations of cone types are established only for the short-wavelength-sensitive (S) cones. The changing distribution in S cone density with eccentricity in the human retina, as determined by morphological criteria (Ahnelt *et al.*, 1987), closely correspond to the psychophysical estimates of the distribution of S cones in human retina (e.g. Williams, MacLeod & Hayhoe, 1981a,b; Castaño & Sperling, 1982), as well as to the distribution found in anatomical studies on other primate retinæ (Marc & Sperling, 1977; de Monasterio, McCrane, Newlander & Schein, 1985).

Morphological characteristics which might distinguish long-wavelength-sensitive (L) and middle-wavelength-sensitive (M) cones have not yet been identified. Recently, psychophysical methods have allowed the estimation of the relative numbers of L and M cones in human fovea centralis (Cicerone & Neger, 1985, 1989a,b; Vimal, Pokorny, Smith & Shevell, 1989). The goal of the present study was to estimate the relative

numbers of L and M cones in eccentric locations of human retina.

Some early psychophysical evidence suggests that the relative numbers of L and M cones may vary with eccentricity. Results from a number of studies, including color naming (Moreland, 1972; Boynton, Schafer & Neun, 1964; Weitzman & Kinney, 1969), color matching (Moreland & Cruz, 1959), wavelength discrimination (Weale, 1951), color perimetry (Connors & Kinney, 1962), and color-discrimination perimetry using Munsell color chips (Uchikawa, Kaiser & Uchikawa, 1982), led to the idea that the peripheral retina tends to exhibit characteristics of deutan color vision defects. The eccentricities at which the peripheral retina was reported to exhibit reduced color discrimination varies among the studies (ranging from 5 to between 20 and 40 deg), possibly due to differences in size, duration, and luminance of the stimuli employed.

Results of more recent psychophysical studies are consistent with stability of the relative numbers of L and M cones with eccentricity. If the size or the intensity of the test field is increased with increasing eccentricity, foveal and eccentric locations show good correspondence for hue naming (Gordon & Abramov, 1977; Abramov & Gordon, 1987; Abramov, Gordon & Chan, 1991), color matching (Stabell & Stabell, 1982a,b), wavelength discrimination (Van Esch, Koldenhof, van Doorn & Koenderink, 1984), and spatiotemporal color discrimination (Noorlander, Koenderink, Den Ouden & Edens, 1983) functions. Measurements of spectral sensitivity (Wooten & Wald, 1973; Wooten, Fuld & Spillman, 1975; Stabell & Stabell, 1984), wavelength discrimination and color matching performance (Stabell & Stabell, 1984), suggest that changes in color perception in the peripheral retina of trichromatic observers may be due to changes in neural organization and not due to a

*The experiments reported here were conducted while the authors were at the University of Colorado, Boulder.

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reduction or loss of one or more of the cone types. The photopic luminous efficiency function has also been shown to remain constant with eccentricity provided reasonable assumptions are made for the density and distribution of the macular pigmentation, and if test fields are scaled according to the cortical magnification factor (Van Esch *et al.*, 1984; Stabell & Stabell, 1984).

In this study we used psychophysical procedures (Cicerone & Nerger, 1985, 1986, 1989a,b) to estimate the relative numbers of L and M cones in the temporal parafoveal retina at eccentricities of 1.0, 1.5, 2.0, 3.0, and 4.0 deg for three color-normal trichromats. A brief report of preliminary results has been presented elsewhere (Nerger & Cicerone, 1987). This report is based on Nerger (1988).

METHODS

Apparatus and stimulus conditions

All experiments were conducted with a standard three-channel Maxwellian-view optical system. Two channels provided adapting background fields subtending 12 deg of visual angle. These channels also provided the broadband bleaching stimuli used to suppress rod signals. The wavelengths of the background fields were varied by interposing interference filters (Ditric Optics) into each channel. Lights from the two channels were optically combined and passed through a clear, glass plate which held three small, opaque fixation dots arranged as shown in Fig. 1. Observers fixated the rightmost point of the fixation display; the monochromatic test (provided by a third channel) was vertically centered between the other two. The retinal location under test was varied from 1.0 to 4.0 deg along the horizontal meridian of the temporal retina by translation of the rightmost point of the fixation display.

FIGURE 1. Schematic diagram of the stimulus conditions. For L cone isolation, a 640 nm test was presented on a 500 nm background field. For M cone isolation, a 520 nm test was presented on a background field composed of a mixture of 460 and 640 nm lights. The rod bleaching paradigm employed in the M cone isolation condition is represented at the bottom of the figure. The fixation target is denoted in the figure by the array of black dots. Observers fixated the rightmost point of the fixation display; the test was vertically centered between the other two.

Using anatomical data on cone density as a guide, the test size was scaled with retinal eccentricity to maintain an approximately equal total number of cones underlying each test stimulus. Precision pinhole apertures (Newport Corporation, PH Series) measuring 84, 188, and 366 μm in dia were used to provide test sizes corresponding to visual angles of 1.87, 4.17, and 8.12 min of arc in dia, respectively, and are referred to nominally as 2.0, 4.0 and 8.0 min of arc. The wavelength of the test was controlled with a grating monochromator (Instruments SA, H-20V). The intensities of the backgrounds and test fields were varied by means of neutral-density filters and wedges.

Probability-of-detection functions were measured for combinations of test and background wavelengths that effectively isolated the responses of the M and L cone classes. For L cone isolation, probability-of-detection functions were measured for a 640 nm test presented on a 500 nm background field. These conditions were chosen to favor detection by the L cones while suppressing the sensitivity of M cones and rods. For M cone isolation, to suppress rod function, observers first viewed a 5.7 log scot td broadband bleaching light which was calculated to bleach 49.2% (according to the measurements of Alpern, 1971) to 54.2% (according to Rushton & Powell, 1972) of rod pigment when viewed for 15 sec. This level corresponds to an elevation in rod absolute threshold of 5.9 log units (Alpern, 1971). A 520 nm test was presented on a chromatic adapting background field composed of a mixture of 460 and 640 nm lights. This combination background field was designed to suppress the sensitivity of rods, S cones, and L cones. The auxiliary adapting field of short-wavelength (460 nm) light was introduced in this set of experiments to selectively reduce the sensitivity of the S cone mechanism.

The observers maintained fixation with the aid of a dental impression bite bar. To further optimize accuracy of fixation, the observers controlled the presentation of the test flash and were instructed to initiate each trial only when confident of proper fixation.

All calibrations were made using a standard radiometer/photometer (EG&G, Model 450).

Observers

Three highly practiced psychophysical observers [two female (CC and VV) and one male (HA)] participated in these experiments. On the basis of anomaloscopic matches and small field color matches, all were diagnosed as having normal trichromatic color vision. Observer CC was emmetropic; VV and HA were each myopic (<2.0 D correction) in the right eye which was used for these experiments. Optical corrections were applied for these two observers.

Procedures

Measurements of probability-of-detection functions. Observers were dark adapted for 15 min after which, in the L cone isolation condition, they viewed the 12 deg chromatic adapting background field for at least 2 min. In the M cone isolation condition, the observers first

viewed the rod bleaching stimulus. Immediately following the bleach, observers viewed the combination background field for 2 min and probability-of-detection functions were obtained in the usual manner. Control experiments showed no changes in threshold due to the background after this period of time. For each observer, the background intensities were adjusted to a level that elevated the cone absolute threshold for the test by 1 log unit. Probability-of-detection functions were measured for a range of intensity levels of the test graded in 0.1 log unit steps. In each block of 20 trials the intensity level of the test was kept constant. Each intensity level was presented 3 times during an experimental session; the order of presentation was randomized.

All stimuli were presented for 50 msec to minimize the effects of eye movements. The use of small, brief test stimuli was also important since results from a number of laboratories indicate that selective-adaptation techniques that adequately isolate foveal cones may be insufficient for isolating parafoveal cones unless short test durations are used (e.g. Haegerstrom-Portnoy, Verdon & Adams, 1988).

The results reported for each observer are based on data collected in 4 experimental sessions at each of 5 retinal eccentricities for a total of 20 sessions per observer.

Determinations of the best-fitting theoretical functions. The best-fitting theoretical functions to our data were computed according to a least-squares criterion using the subroutine *zxssq* from the IMSL Mathematical Library (IMSL, 1984).

RESULTS

Control experiments

Isolation of M cones in extrafoveal regions. Parafoveal regions contain not only L and M cones, but S cones and rods as well, which makes it especially difficult to isolate the M cones. The validity of our model and the conclusions we draw from comparisons of slopes of probability-of-detection functions rely on the extent to which our experimental conditions succeed in isolating single cone classes.

In order to achieve conditions under which detection was most likely to be determined by the M cones alone, we used a combination of a rod bleach and an adapting background. Rods were selectively desensitized by a bleaching stimulus estimated to bleach approx. 50% of the rod pigment. The wavelength of the test was chosen to favor detection by the M cones and was presented upon a background composed of a combination of violet and red lights, chosen to eliminate the contribution of S cones as well as L cones.

Since the 520 nm test, chosen to favor M cone detection, is also an effective stimulus for rods, control experiments were performed to ensure that the bleaching stimulus we chose effectively eliminated rod contribution to the detection of the test. Probability-of-detection functions were measured for a 520 nm test, presented on a background field composed of a mixture of 460 and

FIGURE 2. Upper panel: probability-of-detection data for observer HA measured with a 520 nm test on a background field composed of a mixture of 460 and 640 nm lights are plotted as a function of the log relative quanta per flash. Different symbols denote the different rod bleaching levels. Open circles represent data obtained without a rod bleach; the remaining symbols represent data obtained following exposure durations calculated to bleach 25% (solid squares), 40% (open triangles), or 50% (solid circles) of the rod pigment. Error bars mark ± 1 SEM based on between-session variability. Lower panel: comparison of the probability-of-detection functions measured with a 520 nm (solid circles) and 580 nm (solid triangles) test presented on the M cone isolating background field. Probability of detection is plotted as a function of the intensity of the test flash. Error bars denote ± 1 SEM based on between-session variability.

640 nm lights under four conditions: without a rod bleach, and with rod bleaches calculated to bleach 25, 40 or 50% of the rod pigment. These measurements made for observer HA at 2.0 deg eccentricity are compared in the upper panel of Fig. 2. The slopes of the measured detection functions are seen to be graded according to the effectiveness of the bleaches. The slopes of the functions obtained without the rod bleach and following the 25% rod bleach are each steeper than the slope of the function obtained following the 40 and 50% rod bleaches. This is consistent with more receptors (presumably rods) contributing to detection of the test under conditions without the rod bleach or with a 25% rod bleach as compared with the 40 or 50% rod bleaches. Since the slope of the function obtained following the 40% rod bleach is identical to the slope of the function obtained following the 50% rod bleach, this is consistent with elimination of rod contributions if 40% or more of the rod pigment is bleached. Thus, we have some measure of assurance that by using the 50% bleach

our results are not likely to be contaminated by rod contributions.

In addition, we tracked the time course of sensitivity recovery following the 25, 40, and 50% rod bleaches. After the 50% bleach, thresholds measured for the 520 nm test upon the combination background remained unchanged for 42 min, longer than the time required to complete one set of measurements of the probability-of-detection function. Furthermore, measurements of the spectral sensitivity of the detecting mechanism after the 50% bleach and upon the combination background showed no evidence of a contribution from rods, S cones, or L cones. In line with these results, we used the 50% rod bleaching stimulus for subsequent experiments.

Finally, in order to provide further confirmation that rod or S cone signals did not contribute to detection of the 520 nm test under our M cone isolation condition, we performed an additional control experiment. Probability-of-detection functions were obtained for a 580 nm test presented on the combination background field after the 50% rod bleach, and these measurements were compared to those made with the 520 nm test. If the bleach in combination with the background effectively suppresses the rods and S cones, then the slope of the detection function measured with the 580 nm test should be equal to the slope of the function measured with the 520 nm test. If, on the other hand, rods or S cones contribute to detection of the 520 nm test, then since rods and S cones are much less sensitive to 580 nm light than to 520 nm light, the slope of the function obtained with the 580 nm test should be shallower than the slope obtained with the 520 nm test. The results for observer HA are illustrated in the lower panel of Fig. 2. The identical detection functions provide evidence that we have eliminated rods and S cones from participating in the detection of the test under our M cone isolation conditions.

Although our control experiments confirmed that S cones and rods are not likely to be involved in the detection of the 520 nm test in our M cone isolation condition, there remained a small chance that L cones might have influenced the M cone detection functions. If L cones had contributed to detection of the 520 nm test in any significant way, then the stability of the slope of the detection function obtained with the 580 nm test would not be predicted, since L cones are more sensitive to 580 nm light than to 520 nm light.

We further verified that the M cone isolation condition had not inadvertently, but significantly, reduced the sensitivity of the M cones. If the M cones had been appreciably desensitized, such that the number of active M cone receptors was reduced, then in this case, we would have underestimated the relative number of M cones and consequently overestimated the L to M cone ratio. We believe this is unlikely for a number of reasons. First, our measurements of the percent seen as a function of the intensity of the 520 nm test did not vary with time after bleach, between the first 2 and 42 min after the bleach, the period during which our measurements were made. Second, we conducted control experiments

in which we used a test of 580 nm presented on the M cone isolating background, with or without a prior rod bleach, and obtained detection functions with identical slopes. These results would not be expected if M cones had been significantly desensitized in our experimental paradigm. Finally, it is unlikely the M cones were desensitized by the chromatic background field (460 nm in combination with 640 nm) since probability-of-detection functions show no change of slope over a 10-fold range of intensities of the background.

Relative numbers of M and L cones in extrafoveal regions

Measurements were made under L cone and M cone isolation conditions at retinal eccentricities of 1.0, 1.5, 2.0, 3.0, and 4.0 deg along the horizontal meridian of the temporal retina for three color-normal trichromatic observers. Results for each observer at the five eccentricities we examined are presented graphically in Figs 3, 4, and 5. The test size (2.0, 4.0, or 8.0 min of arc in dia) chosen for measurements at each eccentricity was based on an attempt to equate the total number of cones underlying the test stimulus according to the eccentricity-dependent fall-off in total cone density (Østerberg, 1935; Curcio *et al.*, 1987). In each case, the slope of the probability-of-detection function based on L cone detection is steeper than the slope of the associated function based on M cone detection. This implies that for each observer, at each of these eccentricities, the density of L cones is greater than that of M cones.

Two procedures were used to obtain estimates of the relative numbers of L and M cones contributing to detection at each of the eccentricities examined. The model and its assumptions as well as its application to foveal measurements have been described in previous papers (Cicerone & Nerger, 1989a,b). Briefly, according to the model, the probability of detection $P(x)$ is expressed as follows:

$$P(x) = 1 - Q(x)^N \quad (1)$$

where $Q(x)$ represents the probability that any one of the N illuminated cones did not absorb the required number of quanta and therefore was not activated, and x is the average number of quanta delivered per flash. In our model, we assume the cones function as independent detectors. That is, we assume that the test flash will be detected if any one of the illuminated cones absorbs the required number of quanta.

Equation (1) can be rewritten to express the separate probabilities of detection by the L and M cone populations. Assuming the value of Q for a fixed value of the variable x is the same for L and M cones, the ratio of L to M cones can then be expressed as:

$$\frac{N_L}{N_M} = \frac{dP_L}{dP_M} \frac{1 - P_M}{1 - P_L} \quad (2)$$

This expression thus relates the ratio of the number of L to M cones (N_L/N_M) to the ratio of the slopes (dP_L/dP_M) of the psychophysically-determined probability-of-detection functions P_L and P_M measured

FIGURE 3. Probability-of-detection functions obtained for observer CC at five retinal eccentricities. The eccentricity and diameter of the test in minutes of arc are specified in each panel. Open symbols represent the data obtained under L cone isolation conditions, solid symbols under M cone isolation conditions. Error bars denote ± 1 SEM based on between-session variability. The solid curves drawn through the data are the best-fitting theoretical functions according to our model. The resultant numbers of L cones (N_L) and M cones (N_M) obtained by application of the model are indicated beside the respective functions.

under L and M cone isolation conditions, respectively. Equation (2) was applied to at least three different values of x (the average number of quanta delivered per flash) along the nearly linear portion of each pair of detection functions. The values for N_L/N_M obtained by using equation (2) were then averaged to obtain our first approximations of the L to M cone ratio. These values are recorded in Table 1 under the heading "ratio of slopes."

We achieved a second, more quantitative assessment of the ratio of L to M cones by further assuming that the numbers of incident photons and the numbers of quantal absorptions follow a Poisson process,* i.e.:

$$Q(x) = \sum_{k=0}^{m-1} \frac{e^{-x} x^k}{k!} \quad (3)$$

where m is the number of quanta required to activate a cone. In our model, we further assume that the value for m is the same for the M and L cone types. Using equation (3) in combination with equation (1), we estimated the numbers of L and M cones underlying the test stimulus by finding the values for the parameter N which yielded the best-fitting theoretical functions to our measured detection functions.

Since N and m together determine the slope of the theoretical functions, the estimate of N is dependent on the assumed value of m . Previous application of this model to measurements made in the fovea centralis for the three observers of this study were fit best when $m = 6$ (Cicerone & Nerger, 1989a,b). This is in good agreement with the estimates reported by others (Brindley, 1963; Marriott, 1963; Vimal *et al.*, 1989). We therefore constrained the parameter m to be equal to 6 for the parafovea and found the best-fitting theoretical functions to our data according to a least-squares criterion. The best-fitting theoretical functions are drawn through the data displayed in Figs 3, 4, and 5; the numbers of L cones (N_L) and M cones (N_M) specified by the model are indicated by the respective functions. The ratios of L to M cones achieved by this method are listed in Table 1 under the heading "best-fitting functions."

Figure 6 presents the means of the estimates of the ratio of L to M cones achieved by the two methods for each of our three observers. For each observer, the dashed line marks the mean of the ratios for all eccentricities, including the measurements previously made in the fovea centralis (Cicerone & Nerger, 1989a). It is evident from the data of observers CC and VV that, except for some small deviations, the ratio of L to M cones does not significantly change with eccentricity up to 4.0 deg. For observer HA, however, although the number of L

*Other than quantal variations in light intensity, other sources of randomness (e.g. noise) have not been considered in this model.

FIGURE 4. Probability-of-detection functions measured for observer VV at five retinal eccentricities. The results are plotted as described in Fig. 3.

FIGURE 5. Probability-of-detection functions measured for observer HA at five retinal eccentricities. The results are plotted as described in Fig. 3.

TABLE 1. Summary of the ratios of L to M cones determined for each of the observers at the five parafoveal locations investigated. Estimates derived by the two estimation procedures employed are shown. The first method, labeled "ratio of slopes," estimated the ratio by direct comparisons of the slopes of the measured probability-of-detection functions. The second, labeled "best-fitting functions," estimated the ratio by analyses of the best-fitting theoretical functions to the data.

See text for descriptions of the estimation procedures

		Degrees eccentricity (temporal retina)				
		1.0	1.5	2.0	3.0	4.0
CC	Ratio of slopes	1.92	1.79	1.96	1.98	1.81
	Best-fitting functions	1.91	1.79	1.99	1.73	1.85
VV	Ratio of slopes	1.87	1.73	1.93	2.06	2.24
	Best-fitting functions	1.91	1.82	1.92	1.95	2.15
HA	Ratio of slopes	1.81	1.88	1.71	1.72	1.47
	Best-fitting functions	2.02	2.06	2.00	1.58	1.53

cones always remains greater than the number of M cones, there appears to be a decline in the relative numbers of L cones for eccentricities > 2.0 deg.

DISCUSSION

Our results indicate that for color-normal trichromats, the relative numbers of L and M cones remain approximately invariant from 1.0 to 4.0 deg in the temporal retina. In addition, for each of our observers, the foveal and parafoveal measurements are within the range of values previously obtained in fovea centralis (Cicerone & Nerger, 1989a). These results are in agreement with conclusions drawn from recent studies showing that the

shapes of the photopic luminous efficiency and wavelength discrimination functions remain nearly constant with eccentricity (well beyond 4.0 deg) provided the effects of test size, macular pigmentation, and contributions from S cones are taken into account (Stabell & Stabell, 1984; Van Esch *et al.*, 1984). The foveal photopic luminous efficiency function can be successfully modeled as a weighted combination of the L and M cone spectral sensitivities, where the weights are determined by the relative numbers of these cone types (DeVries, 1946; Rushton & Baker, 1964; Smith & Pokorny, 1975; Cicerone & Nerger, 1989a). A stability in the shape of this function with eccentricity is consistent with stability in the relative numbers of the L and M cone types.

Our results further imply that, barring significant changes in neural connectivity, color perception in the periphery should remain essentially unchanged as compared to the fovea. Indeed, there are recent studies that report a full range of well-saturated hues may be observed even in the extreme periphery provided the intensity and size of the test stimuli are sufficiently scaled (Gordon & Abramov, 1977; Stabell & Stabell, 1982a,b; Abramov & Gordon, 1987; Abramov *et al.*, 1991). For individual observers, the wavelength seen as uniquely yellow, but not that seen as uniquely blue, remains unchanged from fovea to 4.0 deg eccentricity in the temporal retina (Cicerone & Metscher, 1989; Cicerone, 1990). This finding is also consistent with a stable ratio of L to M cones. Other color naming and wavelength discrimination experiments (e.g. Weitzman & Kinney, 1969; Boynton *et al.*, 1964), which have provided evidence that the peripheral retina exhibits reduced hue discrimination, especially in mid-spectral regions, did not systematically investigate the effects of scaling the size or intensity of the test with increasing eccentricity.

Changes in neural connectivity may occur in the peripheral retina, with or without changes in the relative numbers of the different cone types. Recent investigations suggest a single scaling factor, such as cortical magnification, may not be adequate to describe differences in color appearance (Abramov & Gordon, 1988) and differences in the absolute sensitivities of Stiles' π_4 and π_5 mechanisms (Buck, Bonnelle, Zohn & Knight, 1988) with increasing eccentricity. Buck *et al.* (1988) report, however, that the differences in π_4 and π_5 measured at the fovea and at 7.0 deg eccentricity can be accounted for by a combination of size and sensitivity scaling. Since the magnitude of the scaling factors required to equate increment sensitivity was found to be similar for π_4 and π_5 , the results of Buck *et al.* are consistent with no change in the relative densities of M and L cones from the fovea to 7.0 deg eccentricity.

Individual differences between observers

Although the results of observers CC and VV are consistent with stability in the relative numbers of L and M cones from the fovea centralis to 4.0 deg eccentricity, observer HA's results indicate a decline in the ratio beyond approx. 2.0 deg eccentricity (Fig. 6). The slopes of the best-fitting straight lines are -0.046 for the data

FIGURE 6. Estimated ratios of L to M cones as a function of retinal eccentricity. Different symbols represent the different observers. Error bars denote ± 1 SEM based on the two estimation procedures employed (see text for descriptions). For each observer, the dashed lines are drawn through the means of the ratios determined from the fovea centralis (Cicerone & Nerger, 1989) to 4.0 deg eccentricity. Except for some local deviations, the estimates of the relative numbers of M and L cones remain approximately invariant.

of CC, +0.009 for VV, and -0.130 for HA. Standard non-directional statistical tests for differences in slopes were applied to the results and these revealed no significant differences between the slopes of the best-fitting straight lines to the data of observers CC and VV and a line of slope equal to zero ($P > 0.09$). The slope of the best-fitting straight line to the data of HA is significantly different from a line of slope equal to zero ($P \leq 0.05$), however, the decline in the ratio is only apparent in the estimates made at 3.0 and 4.0 deg eccentricity. Overall, the conclusion we draw is that our results are most consistent with no change in the relative numbers of L and M cones in the eccentricity range we have investigated.

Estimates of total (M + L) cone density

We estimated the total number of cones contributing to detection of our test stimuli for each observer by summing the numbers of L and M cones obtained by our second estimation procedure. The retinal areas illuminated by our test stimuli were estimated by using the optical spread function of the human eye measured at the fovea (Campbell & Gubisch, 1966; Gubisch, 1967) and assuming an axial focal length of 16.667 mm (LeGrand, 1957). We assumed an effective image which was uniformly lit and with a diameter defined by the point at which illumination in the scatter profile fell to e^{-1} of the maximal value. This is a conservative modification of the cylindrical approximation proposed by Vos, Walraven and van Meeteren (1976). Under our assumptions, our test stimuli which measured 1.87, 4.17, and 8.12 min of arc in dia were calculated to illuminate retinal areas of 141, 468, and $1496 \mu\text{m}^2$, respectively.

Given our estimates for the total number of cones illuminated by the test stimuli and the corresponding retinal image sizes, we calculated the total (M + L) cone densities for each of our observers at each of the five eccentricities investigated. Estimates of M + L cone densities per mm^2 at 1.0, 1.5, 2.0, 3.0, and 4.0 deg eccentricity for our three observers were 30,900, 29,900, 21,700, 18,400, and 9,400, respectively for observer CC; 46,200, 16,400, 21,300, 17,000, and 12,600 for observer VV; and 29,600, 17,700, 12,800, 10,500, and 7,300 for observer HA. The mean values and standard errors of the mean based on between-observer variability are shown in Fig. 7.

Comparison to other estimates

We used the psychophysical estimates of extrafoveal cone spacing provided by Williams (1988) to obtain another approximation of the total M + L cone density per mm^2 . The mean data of Williams, based on laser interferometric techniques which exclude S cones, are shown to be in reasonable agreement with our measurements (Fig. 7). Consistent with the well-documented lower density of cones in temporal retina (Østerberg, 1935; Perry & Cowey, 1985; Curcio *et al.*, 1987), our measurements in temporal retina fall slightly below those derived from Williams' measurements which were not confined to the temporal retina.

FIGURE 7. Plotted are the means of the M + L cone densities estimated for our three trichromatic observers (solid circles) at eccentricities ranging from 1.0 to 4.0 deg along the horizontal meridian of the temporal retina. The error bars denote ± 1 SEM based on between-observer variability. These estimated densities are compared to the means of the M + L cone densities implied by the anatomical investigations of Østerberg (1935) (open circles) and Curcio *et al.* (1987) (open squares) which have been corrected for the density of S cones (Ahnelt *et al.*, 1987). Also shown are estimates of M + L cone densities derived from the psychophysical measurements of Williams (1988) (open triangles).

In order to make an appropriate comparison to the anatomical measurements of total cone density (Østerberg, 1935; Curcio *et al.*, 1987), we applied a correction to the anatomical data for the number of S cones at each eccentricity. This is especially of concern in the region of 1.0–2.0 deg, which contains the highest density of S cones (e.g. Ahnelt *et al.*, 1987). We estimated the density of S cones according to the results of Ahnelt *et al.* (1987), who report S cones represent 15% of the total cone population at approx. 1.0 deg and decrease to between 7 and 8% at 10 deg eccentricity. We further assumed that S cone density declines exponentially within this range, as has been described in the macaque retina (de Monasterio *et al.*, 1985). The calculated S cone densities were used to compute the expected M + L cone densities from the data in the literature. These corrected anatomical values are also plotted in Fig. 7.

The overall pattern of results for each of our observers parallels the eccentricity-dependent fall-off in the total cone density seen in the anatomical data. The mean cone densities estimated from our results in the parafovea fall near Østerberg's (1935) anatomical measurements. Our results for the fovea centralis (Cicerone & Nerger, 1989a) were also in good agreement with the anatomical results of Østerberg (1935) as well as those of Miller (1979). At each eccentricity the measurements of Curcio *et al.* (1987) generally exceed the other estimates. The differences may represent individual variability, inasmuch as the total number of individuals for whom anatomical

data are available is five and our psychophysical results report data from three observers.

Our psychophysical estimates of the total density of L and M cones can be affected by a number of factors. For example, estimates of total cone density are moderately sensitive to the assumed value of the axial focal length of the eye. If we had adopted Drasdo and Fowler's (1974) value of 16.041 mm, as Curcio *et al.* (1987) did, instead of LeGrand's (1957) value of 16.667 mm, our estimates of the L + M cone densities would increase by approx. 8%. Another factor which could influence our results is the specific detection criterion adopted by each of our observers, since this could affect the steepness of the slope of the detection functions. It is important to note, however, that unless these factors differentially affect our results in the M cone isolation as compared to the L cone isolation conditions, our estimates of the L to M cone ratio should not be affected.

Our estimates of the total numbers of M and L cones contributing to detection of our test stimuli may be underestimated if the detection thresholds are determined by postreceptoral neurons receiving input from multiple receptors rather than by single cones. If this were the case, then according to our model, our procedures would be likely to estimate the number of these postreceptoral neurons rather than the number of cones, and the cone density would thus be underestimated. In this regard, we note that our estimates are lower than the mean of the anatomical measurements, corrected for S cones, by approximately a factor of 1.5 at each eccentricity. A number of anatomical studies report evidence for many-to-one connections of photoreceptors to bipolar cells (Boycott & Dowling, 1969; Kolb, 1970), however, midget bipolars, which synapse with only a single cone, have been identified in rhesus monkey retina from the fovea centralis to beyond 5 deg eccentricity (Kolb, Boycott & Dowling, 1969). Some midget ganglion cells in peripheral human retina retain small dendritic fields, suggesting that these cells may receive input from only one bipolar cell (Rodieck, Binmoeller & Dineen, 1985). Furthermore, one-to-one contacts between midget bipolars and midget ganglion cells have been identified out to at least 10 deg in the human peripheral retina (Kolb & DeKorver, 1988). Certainly, our estimates of the relative numbers of L and M cones should be unaffected by postreceptoral summation provided that postreceptoral neurons receive segregated inputs from the same number of L or M cones. In this case, the relative numbers of postreceptoral neurons receiving from L cones as compared to those receiving from M cones should be the same as the ratio of L to M cones.

In summary, our psychophysically-based estimates of the L to M cone ratio indicate the ratio remains approximately invariant from 1.0 to 4.0 deg in the temporal retina of color-normal trichromats, with a mean ratio of approximately two L cones for each M cone. The value obtained for each of our three observers was close to the measurements previously obtained in fovea centralis (Cicerone & Nerger, 1989a).

REFERENCES

- Abramov, I. & Gordon, J. (1987). Color appearance in central and peripheral retina. *Journal of the Optical Society of America, A*, 4, 38.
- Abramov, I. & Gordon, J. (1988). Color appearance in peripheral retina: Naso-temporal asymmetries. *Investigative Ophthalmology and Visual Science*, 29 (Suppl.), 300.
- Abramov, I., Gordon, J. & Chan, H. (1991). Color appearance in the peripheral retina: Effects of stimulus size. *Journal of the Optical Society of America, A*, 8, 404–414.
- Ahnelt, P. K., Kolb, H. & Pflug, R. (1987). Identification of a subtype of cone photoreceptor, likely to be blue sensitive, in the human retina. *Journal of Comparative Neurology*, 225, 18–34.
- Alpern, M. (1971). Rhodopsin kinetics in the human eye. *Journal of Physiology*, 217, 447–471.
- Boycott, B. B. & Dowling, J. D. (1969). Organization of the primate retina: Light microscopy. *Philosophical Transactions of the Royal Society B*, 255, 109–184.
- Boynton, R. M., Schafer, W. & Neun, M. E. (1964). Hue-wavelength relation measured by color-naming method for three retinal locations. *Science*, 146, 666–668.
- Brindley, G. S. (1963). The relation of frequency of detection to intensity of stimulus for a system of many independent detectors each of which is stimulated by m-quantum coincidence. *Journal of Physiology*, 169, 412–415.
- Buck, S. L., Bonnelle, K., Zohn, P. & Knight, R. (1988). Size and sensitivity (M- and F-) scaling of π -4 and π -5. Presented at the 1988 annual meeting of the Optical Society of America, Santa Clara, Calif.
- Campbell, F. W. & Gubisch, R. W. (1966). Optical quality of the human eye. *Journal of Physiology, London*, 186, 558–578.
- Castaño, J. A. & Sperling, H. G. (1982). Sensitivity of the blue-sensitive cones across the central retina. *Vision Research*, 22, 661–673.
- Cicerone, C. M. (1990). Color appearance and the cone mosaic in trichromacy and dichromacy. In Ohta, Y. (Ed.), *Color vision deficiencies* (pp. 1–12). Amsterdam: Kugler & Ghedini.
- Cicerone, C. M. & Metscher, B. D. (1989). Variations in the cone populations and related changes in color perception with eccentricity in the human retina. *Investigative Ophthalmology and Visual Science* 30 (Suppl.), 53.
- Cicerone, C. M. & Nerger, J. L. (1985). The ratio of long-wavelength-sensitive to middle-wavelength-sensitive cones in the human fovea. *Investigative Ophthalmology and Visual Science*, 26 (Suppl.), 11.
- Cicerone, C. M. & Nerger, J. L. (1986). The density of cones in the dichromatic fovea. *Investigative Ophthalmology and Visual Science*, 27 (Suppl.), 292.
- Cicerone, C. M. & Nerger, J. L. (1989a). The relative numbers of long-wavelength-sensitive to middle-wavelength-sensitive cones in the human fovea centralis. *Vision Research*, 29, 115–128.
- Cicerone, C. M. & Nerger, J. L. (1989b). The density of cones in the fovea centralis of the human dichromat. *Vision Research*, 29, 1587–1595.
- Connors, M. M. & Kinney, J. A. S. (1962). Relative red-green sensitivity as a function of retinal position. *Journal of the Optical Society of America*, 52, 81–84.
- Curcio, C. A., Sloan, K. R. Jr, Kalina, R. E. & Hendrickson, A. E. (1990). Human photoreceptor topography. *Journal of Comparative Neurology*, 292, 497–523.
- Curcio, C. A., Sloan, K. R. Jr, Packer, O., Hendrickson, A. E. & Kalina, R. E. (1987). Distribution of cones in human and monkey retina: Individual variability and radial asymmetry. *Science*, 236, 579–582.
- DeVries, H. L. (1946). Luminosity curves of trichromats. *Nature, London*, 157, 736–737.
- Drasdo, N. & Fowler, C. W. (1974). Non-linear projection of the retinal image in a wide-angle schematic eye. *British Journal of Ophthalmology*, 58, 709–714.
- Gordon, J. & Abramov, I. (1977). Color vision in the peripheral retina. II. Hue and saturation. *Journal of the Optical Society of America*, 67, 202–206.

- Gubisch, R. W. (1967). Optical performance of the human eye. *Journal of the Optical Society of America*, 57, 407–415.
- Haegerstrom-Portnoy, G., Verdon, W. & Adams, A. J. (1988). Cone interaction occurs in the parafovea under $\pi 4$ stimulus conditions. *Vision Research*, 28, 397–406.
- IMSL Mathematical Library (1984). IMSL, Houston, Tx.
- Kolb, H. (1970). Organization of the outer plexiform layer of the primate retina: Electron microscopy of Golgi-impregnated cells. *Philosophical Transactions of the Royal Society B*, 258, 261–283.
- Kolb, H. & DeKorver, L. (1988). Synaptic input to midget ganglion cells of the human retina. *Investigative Ophthalmology and Visual Science*, 29 (Suppl.), 326.
- Kolb, H., Boycott, B. B. & Dowling, J. E. (1969). A second type of midget bipolar cell in the primate retina. *Philosophical Transactions of the Royal Society B*, 255, 177–184.
- LeGrand, Y. (1957). *Light, colour, and vision*. New York: Wiley.
- Marc, R. E. & Sperling, H. G. (1977). Chromatic organization of primate cones. *Science*, 196, 454–456.
- Marriott, F. H. C. (1963). The foveal absolute visual threshold for short flashes and small fields. *Journal of Physiology*, 169, 416–423.
- Miller, W. H. (1979). Ocular optical filtering. In Autrum, H. (Ed.), *Handbook of sensory physiology*, (Vol. VII/6A, Chap. 3). Berlin: Springer.
- de Monasterio, F. M., McCrane, E. P., Newlander, J. K. & Schein, S. J. (1985). Density profile of blue-sensitive cones along the horizontal meridian of macaque retina. *Investigative Ophthalmology and Visual Science* 26 (Suppl.), 289–302.
- Moreland, J. D. (1972). Peripheral colour vision. In Jameson, D. & Hurvich, L. M. (Eds), *Handbook of sensory physiology* (Vol VII/4, Chap. 20). Berlin: Springer.
- Moreland, J. D. & Cruz, A. (1959). Colour perception with the peripheral retina. *Optica Acta*, 6, 117–151.
- Nerger, J. L. (1988). The relative numbers of long-wavelength-sensitive to middle-wavelength-sensitive cones in the human fovea and parafovea. Ph.D. dissertation, University of California, San Diego, Calif.
- Nerger, J. L. & Cicerone, C. M. (1987). The relative numbers of long-wavelength-sensitive (L) and middle-wavelength-sensitive (M) cones in the human parafoveal retina. *Journal of the Optical Society of America*, A, 4, 122.
- Noorlander, C., Koenderink, J. J., Den Ouden, R. J. & Edens, B. W. (1983). Sensitivity to spatiotemporal colour contrast in the peripheral visual field. *Vision Research*, 23, 1–11.
- Østerberg, G. (1935). Topography of the layer of rods and cones in the human retina. *Acta Ophthalmologica*, VI (Suppl.), 3–103.
- Perry, V. H. & Cowey, A. (1985). The ganglion cell and cone distributions in the monkey's retina: Implications for central magnification factors. *Vision Research*, 25, 1795–1810.
- Rodieck, R. W., Binmoeller, K. F. & Dineen, J. (1985). Parasol and midget ganglion cells of the human retina. *Journal of Comparative Neurology*, 233, 115–132.
- Rushton, W. H. A. & Baker, H. D. (1964). Red/green sensitivity in normal vision. *Vision Research*, 4, 75–85.
- Rushton, W. A. H. & Powell, D. S. (1972). The rhodopsin content and the visual threshold of human rods. *Vision Research*, 12, 1073–1081.
- Smith, V. C. & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research*, 15, 161–171.
- Stabell, B. & Stabell, U. (1982a). Bezold-Brücke phenomenon of the far peripheral retina. *Vision Research*, 22, 845–849.
- Stabell, U. & Stabell, B. (1982b). Color vision in the peripheral retina under photopic conditions. *Vision Research*, 22, 839–844.
- Stabell, U. & Stabell, B. (1984). Color-vision mechanisms of the extrafoveal retina. *Vision Research*, 24, 1969–1975.
- Uchikawa, H., Kaiser, P. K. & Uchikawa, K. (1982). Color-discrimination perimetry. *Color*, 7, 264–272.
- Van Esch, J. A., Koldenhof, E. E., van Doorn, A. J. & Koenderink, J. J. (1984). Spectral sensitivity and wavelength discrimination of the human peripheral visual field. *Journal of the Optical Society of America*, A, 1, 443–450.
- Vimal, R. L. P., Pokorny, J., Smith, V. C. & Shevell S. K. (1989). Foveal cone thresholds. *Vision Research*, 29, 61–78.
- Vos, J. J., Walraven, J. & van Meeteren, A. (1976). Light profiles of the foveal image of a point source. *Vision Research*, 16, 215–219.
- Weale, R. A. (1951). Hue-discrimination in para-central parts of the human retina measured at different luminance levels. *Journal of Physiology*, 113, 115–122.
- Weitzman, D. O. & Kinney, J. A. S. (1969). Effect of stimulus size, duration, and retinal location upon the appearance of color. *Journal of the Optical Society of America*, 59, 640–643.
- Williams, D. R. (1988). Topography of the foveal cone mosaic in the living human eye. *Vision Research*, 28, 433–454.
- Williams, D. R., MacLeod, D. I. A. & Hayhoe, M. M. (1981a). Foveal tritanopia. *Vision Research*, 21, 1341–1356.
- Williams, D. R., MacLeod, D. I. A. & Hayhoe, M. M. (1981b). Punctate sensitivity of the blue-sensitive mechanism. *Vision Research*, 21, 1357–1375.
- Wooten, B. R. & Wald, G. (1973). Color-vision mechanisms in the peripheral retinas of normal and dichromatic observers. *Journal of General Physiology*, 61, 125–145.
- Wooten, B. R., Fuld, K. & Spillman, L. (1975). Photopic spectral sensitivity of the peripheral retina. *Journal of the Optical Society of America*, 65, 334–342.

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