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THE DENSITY OF CONES IN THE FOVEA CENTRALIS OF THE HUMAN DICHROMAT

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Abstract—We present estimates, based on psychophysical measurements, of the density of cones in the fovea centralis of human dichromats. The estimates for a group of three protanopes and three deuteranopes (this study) were compared to the estimates of the density of cones in a group of six color normal trichromats from previous studies (Cicerone & Nerger, 1985, 1989). The results support the conclusion that the density of cones in the fovea centralis of the dichromat is comparable to that of the color normal trichomat. These results tend not to support a model of dichromacy in which a class of cones as well as the associated pigment are lost in the dichromatic eye. Instead, dichromacy appears to involve a loss of one of the three visual pigments associated with human trichromacy, with a retention of the full numbers of cones.

Cones Human fovea centralis Dichromats

INTRODUCTION

Dichromats are generally acknowledged to lack one of the three cone pigments present in the color normal trichromatic retina. A number of studies have combined to provide nearly incontrovertible evidence to support this deficiency as the basis for the reduced capability of dichromats to make color discriminations. The results of color matching (Maxwell, 1855; Pitt, 1944; Wright, 1946) selective adaptation (Wald, 1964, 1966), and retinal densitometric (Rushton, 1963, 1965; Alpern & Wake, 1977) experiments are consistent with this interpretation. Within this framework, two general models of dichromacy remain tenable. One model species that a class of cones as well as the associated pigment are lost in the dichromatic eye, and a second that one of the three cone pigments is lost while the number of cones remains undiminished. If the first of these models is correct, one might expect the density as well as the numerosity of cones in the dichromatic eye to be less than that in the trichromatic eye, and the grain of the cone mosaic of the dichromatic fovea might be expected to be coarser. According to the second model, the numerosity and density of cones in the dichromatic fovea should equal that in the trichromatic fovea.

Under the assumption that a reduced number of cones would imply poorer acuity, Hecht (1949) tried to resolve this question by obtaining standard acuity measurements on dichromats. Although the results of Hecht's (1949) experiments tended to favor the first of the models in that he obtained poorer acuity for dichromats, subsequent experiments by others (Brown, Kuhns & Adler, 1957; Brown, Phares & Fletcher, 1960; Verriest, 1958; Wilder, 1970) have not consistently substantiated Hecht's results. Wilder (1970), for example, found that as compared to trichromats, deuteranopes showed greater acuity as measured by detection of the gap in a Landolt C at all test wavelengths, whereas protanopes showed enhanced acuity for measurements in the blue and green regions of the spectrum, but not for measurements made in the red. Thus, the question of which model of dichromacy is to be preferred has not been adequately resolved with standard measures of acuity. It should also be noted that standard acuity measures may not be capable of detecting the kinds of fine-grained differences at the level of the cone mosaic which would be indicated by the two competing models, inasmuch as the gap to be detected in the standard Landolt C is many minutes of arc in visual angle and spans many cones in the densely-packed foveal mosaic in the human eye, where the center-to-center spacing of cones is known to be a mere 0.6 min of arc or less (Osterberg, 1935; Miller, 1979; Ahnelt, Kolb & Pflug, 1987; Curcio, Sloan, Packer, Hendrickson & Kalina, 1987).

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In this work, we describe a more direct approach to estimating the numerosity and density of cones in the dichromatic fovea. Our experiments are based on the detection of tiny test spots of one min in visual angle, which are estimated to illuminate no more than five to seven cones when cast upon the receptor mosaic of the fovea centralis of color normal trichromats. If a class of cones as well as the associated pigment are lost in dichromats and there is a less dense packing of the foveal cone mosaic, the detection of such a tiny test light should be measurably worse for the dichromat as compared to the trichromat, since the dichromat would have fewer cones catching quanta. Moreover, under conditions of chromatic adaptation, which favor detection by the long-wavelength-sensitive (L) cones of the trichromat, it can be predicted that the deuteranope's detection function should match that of the trichromat, since only L cones are retained in the deuteranope's retina according to this model. Similarly, under conditions favoring detection by the middle-wavelength-sensitive (M) cones of the trichromat, the protanope's detection function should be matched. On the other hand, if only a pigment is lost and the full complement of numbers of cones is retained, then the dichromat's detection function, which is based on a larger number of cones, should be steeper than either of the trichromatic functions obtained under these conditions of selective adaptation. Furthermore, the protanope's detection function should be similar to the deuteranope's. Figure 1 illustrates these ideas. Our experiments tested these predictions directly for three deuteranopes and three protanopes as compared to six color normal trichromats. A brief report based on the results of four of these six dichromats has been previously presented (Cicerone & Nerger, 1986).

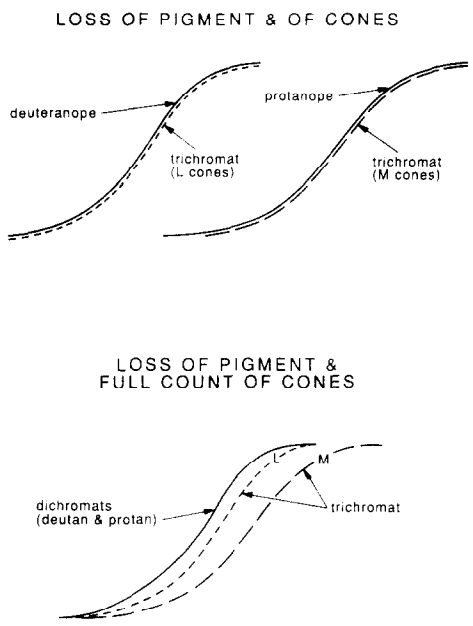

Fig. 1. Shown here are the distinct predictions made by two tenable models of human dichromacy. If, according to the first model (top), a class of cones as well as the associated pigment are lost in the dichromat, then the detection of a tiny test light (1 min arc, for our experiments) should be measurably worse for a dichromat as compared to a trichromat. Specifically, under conditions designed to favor detection by L cones, the deuteranope's detection function should match that of the trichromat measured under the same conditions, since the deuteranope's retina retains only the numbers of L cones present in the trichromat. Similarly, the protanope's detection function should provide a match to the trichromat's function measured under conditions designed to favor detection by M cones. According to the second model (bottom), only a pigment is lost and the full complement of numbers of cones is retained. This model predicts that the dichromat's detection function should be steeper than that for the trichromat measured under either L or M cone isolation conditions.

METHODS

Observers

Three deuteranopes and three protanopes served as observers. Their selection was based on anomaloscope matches, neutral point matches to white, and small field color matches, all of which consistently confirmed the classifications of dichromacy. The results for these dichromats were compared to those of six color normal trichromatic observers whose results have been presented in detail elsewhere (Cicerone & Nerger, 1985, 1989). Four of six dichromats and four of six trichromats were emmetropic. The remaining two dichromats (LH and KG) and two trichromat (VV and HA) were mildly myopic and optical corrections were applied for these observers.

Apparatus

A two-channel Maxwellian view apparatus was employed in these experiments. One channel provided the background field which subtended 12 deg of visual angle. Interference filters (Ditric Optics) were used to change the wavelength of the background field. Placed in this channel was a glass plate with four small, opaque fixation dots arranged as the corners of a square whose diagonal extent spanned 3 deg of visual angle. The second channel provided

the test field (precision pinhole aperatures, Newport Corporation, PH series) of one or two min visual angle which appeared in the center of the array of fixation points for a duration of 50 msec. The wavelength of the test was controlled with a monochromator (Instruments SA, H-20V). The intensity of light in the two channels was controlled by means of neutral density filters and wedges. The exit pupil of the Maxwellian view system was 1.9 mm in extent and was centered in the natural pupil, which, for the background illumination we used, was observed to be no less than 3–4 mm in diameter. A standard radiometer/photometer (EG&G, 450) was used for all calibrations. All optical components, as well as the bite bar, were firmly anchored to an optical table (Newport Corporation, MS series). The control of the experiment was aided by a computer (Apple IIE). The apparatus has previously been described in detail (Cicerone & Nerger, 1989).

Procedures

The observer was dark adapted for 15 min. This was followed by a 5 min period of adaptation to the background light. The observer's task was to detect the tiny test light. The observer was instructed to initiate each trial by pressing a button when he was ready and confident of accurate fixation. After presentation of the test light the observer indicated whether the light was seen or not. The main experiments was conducted after two to three preliminary sessions which familiarized the observers to the task.

Two conditions were presented in each experimental session. In one condition the test wavelength was 520 nm and the background wavelength was 640 nm to provide the conditions which would favor *M* cone detection for the trichromat. In the second condition, the test wavelength was 640 nm and the background was 520 nm, which would favor detection by the *L* cones for the trichromatic observer. The background intensity was set so as to raise the threshold for the test 0.5 log unit above its dark-adapted value. The order of presentation of these conditions was randomized from session to session. Presented during each session and for each condition were 8–10 intensity levels, graded in approx. 0.1 log unit steps. Stimuli were presented in blocks of 20 trials with the stimulus intensity held constant in each block of trials. A random assignment of stimulus intensity was made for each block, until each test intensity had been presented for at least 40 trials. Each data point plotted in the results section was based upon at least 120 trials, collected over three to four experimental sessions. Mean values and the associated standard errors of the mean were calculated over sessions.

Determinations of the best-fitting theoretical functions (Cicerone & Nerger, 1989 and as described below) for our measurements were made by a least-squares method ("zxssqz" subroutine from the IMSL Mathematical Library).

RESULTS

The effects of variations in test and background wavelengths

We first conducted experiments which were in the nature of controls and were designed to lay the groundwork for the main experiments, those aimed at comparing the dichromatic to the trichromatic results.

First, probability of detection functions were measured under *M* cone and *L* cone isolation conditions for the dichromatic observers. Shown in Fig. 2 are the results for three deuteranopes. The background intensity levels were chosen to elevate thresholds by 0.5 log unit above the dark adapted value for detecting the test. If these observers are indeed dichromatic, then they should have only one pigment operating in this wavelength range, and the two functions should be identical. As shown in Fig. 2, this was confirmed. Figure 3 shows similar results for the three protanopes we tested. The qualitative comparisons made in Figs 2 and 3 will be made in a more quantitative way by comparing the numbers of cones which we estimate, by means of our model, to contribute to detection of the test under these two conditions (see Table 1 to follow).

Comparison of dichromatic and trichromatic foveal cone densities

We next compared results obtained for these dichromatic observers against those we had previously obtained for trichromatic observers (Cicerone & Nerger, 1985, 1989). The results for all of our observers are presented subsequently in Table 1. The results for deuteranope LH as compared to the results for trichromat CC are shown at the top of Fig. 4; and at the bottom protanope PR is compared to CC. Neither dichromat's results match the trichromat's results under *L* or *M* cone isolation conditions. Instead the dichromatic detection functions are

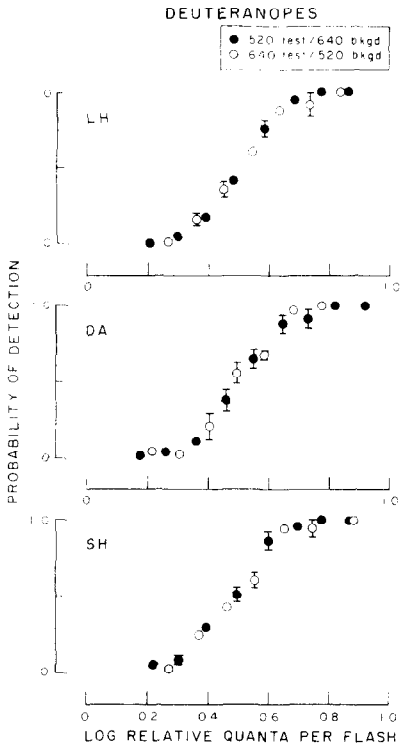

Fig. 2. Probabilities of detection as a function of the number of quanta delivered by the test are plotted for three deuteranopes. Tests were detected under conditions which, for the trichromat, would isolated M (●, 520 nm test upon a 640 nm background) or L (○, 640 nm test upon a 520 nm background) cones. The background levels were chosen to elevate thresholds for the test by 0.5 log unit above the dark-adapted value. The functions measured under M cone isolation conditions are shown to be identical to those measured under L cone isolation conditions.

steeper. This indicates that the number of cones illuminated by the test in the center of the dichromatic fovea is greater than either the number of L cones alone or the number of M cones alone illuminated by the test in the trichromatic fovea.

In order to obtain a more quantitative comparison of the density of cones in the fovea centralis of dichromats and trichromats, we used a model (Cicerone & Nerger, 1989) which allows us to estimate the number of cones contributing to the detection of a small test spot by determining the theoretical function which best fits the measured detection function. The model for detection of tiny tests can be expressed as follows:

$$P(x) = 1 - Q(x)^N,$$

where P, the probability of detection, is expressed in terms Q, the probability that any one of N cones has not caught sufficient quanta to be activated. According to this model, the steeper the measured function, the greater the number of cones contributing to detection. With the added assumption that the absorption of quanta by a cone follows a Poisson process, we further specify that:

$$Q(x) = \Sigma(e^{-x}x^k/k!);$$

where the summation runs from $k = 0$ to $k = (m - 1)$, and m is the number of quanta required to activate a cone. Our measurements were best fit by a choice of m equal to 6. The best-fitting theoretical functions are shown in Fig. 4. The number of cones specified by the fits of the model to these data yield, as an estimate of the numbers of cones contributing to detection of the same-sized test of 1 min in visual angle, 6.41 cones for this deuteranope, 6.26 cones for this protanope, and a sum of 6.01 L and M cones for this trichromat.

Table 1 shows results obtained from the six dichromats in our study as compared to the results previously obtained for six trichromats (Cicerone & Nerger, 1989). The estimate of total number of cones illuminated by a test subtending 1 min of visual angle was calculated for each of the trichromatic observers by summing the estimates obtained under L and M cone

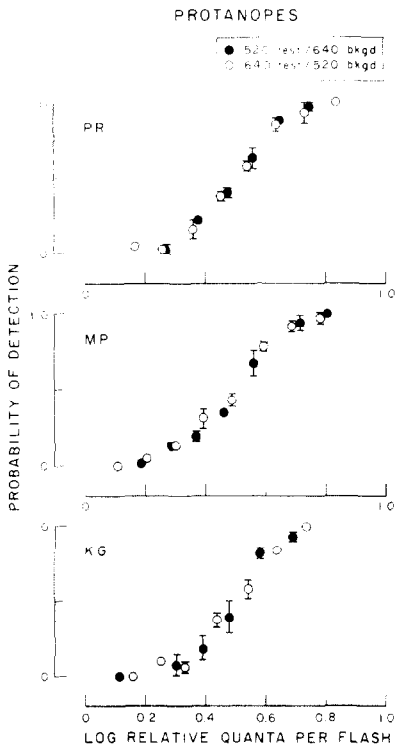

Fig. 3. Results for three protanopes are displayed. All symbols and conditions are as for Fig. 2.

isolation conditions. The estimate for each dichromat was obtained as the mean value of two estimates, one made with the 520 nm test on the 640 nm background and the other with the 640 nm test on the 520 nm background. The group averages of numbers of cones illuminated by a test subtending 1 min of visual angle was estimated to be 5.99 (SEM 0.17) for trichromats, 6.40 (SEM 0.20) for deuteranopes, and 6.33 (SEM 0.11) for protanopes.

These results are consistent with the conclusion that the density of cones in fovea centralis of dichromats is similar to that of trichromats. There may be an objection to this conclusion on the grounds that the procedures for measurement are not quite the same, inasmuch as the cone isolation procedure is designed to exclude a class of cones, either L or

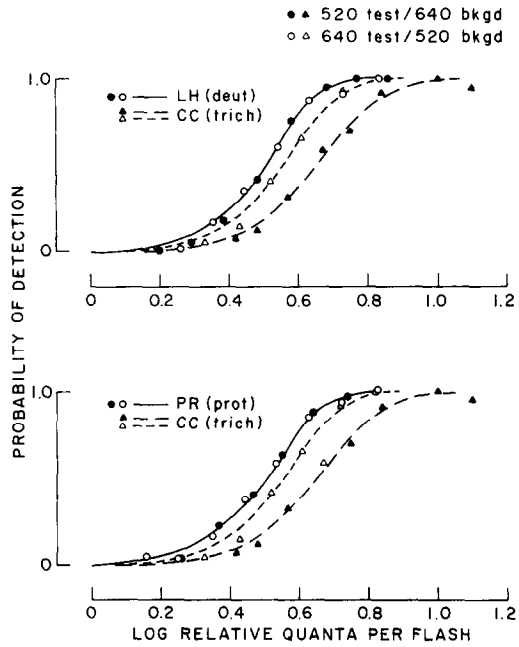

Fig. 4. The results of deuteranope LH are compared to those of color normal trichomat CC at the top, and protanope PR is compared to CC at the bottom. Probability of detection is plotted as a function of the number of quanta delivered by the test of 1 min in visual angle. Neither dichromat's results match the trichromat's results under L or M cone isolation conditions. Instead the the dichromatic detection functions are clearly steeper. This indicates that the number of cones contributing to the detection of the test in the dichromat's fovea centralis is greater than either the number of L cones alone or the number of M cones alone contributing to the detection of the same size test in the trichromatic fovea. The smooth curves drawn through the data sets are the best-fitting functions according to our model for detection (see text). The fits of our model to these data indicate that 6.41 cones contribute to the detection of the test for this deuteranope, 6.26 cones for this protanope, and a sum of 6.01 L and M cones for this trichromat.

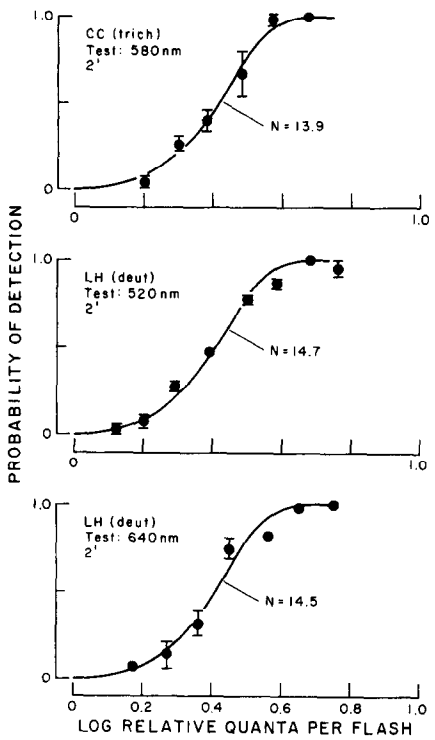

Fig. 5. The top panel shows measurements of probability of detection as a function of the number of quanta delivered by a test flash subtending 2 min of visual angle and of 580 nm for trichromatic observer CC. The wavelength of the test was chosen so as to allow both L and M cones to contribute to detection. The best-fitting theoretical function (see text for the model) is shown as the smooth curve. The number of L and M cones contributing to the detection of the test, according to the model, is 13.9. Shown in the middle (520 nm test) and bottom (640 nm test) panel are the results for deuteranope LH for a test subtending 2 min of visual angle. The numbers of cones specified by the fits of our model to LH's results are 14.7 and 14.5, respectively for the 520 nm and the 640 nm tests. Thus, under conditions which allow both L and M cones of the trichromat to contribute to detection of the test, we estimate that the density of cones in the trichromatic fovea centralis matches that of the dichromat.

M, from contributing to detection for the trichromat. Such is not the case for the dichromat. In order to meet this objection, the following experiment was conducted. For one of our trichromatic observers, we measured detection under conditions in which both L and M cones are expected to contribute to detection. For this purpose, we used a 580 nm test light which subtended 2 min of visual angle. The results of this experiment are shown at the top of Fig. 5. Also shown in this figure is the best-fitting theoretical function which yields a value of 13.9 cones contributing to detection for this size test when both L and M cones contribute to detection. In addition, shown in Fig. 5 are the results

Table 1. Shown are the estimated number of cones contributing to the detection of a test subtending 1 min in visual angle and presented to the fovea centralis of 6 color normal trichromats, 3 deuteranopes and 3 protanopes. The estimates for the trichromats were obtained as the sum of the estimates made under L and M cone isolation conditions. The estimates for the dichromats were calculated as the average value of two estimates, one made with a 520 nm test upon a 640 nm background and the other with a 640 nm test upon a 520 nm background. The mean value for this sample of 6 trichromats was 5.99 (SEM 0.17), that for the 3 deuteranopes was 6.40 (SEM 0.20), and that for the 3 protanopes was 6.33 (SEM 0.11)

Test λ/Bkgd λ		520/640	640/520	Total cones
Trichromats	CC	1.96	4.05	6.01
	JN	1.91	3.80	5.71
	YP	2.54	3.83	6.37
	EM	1.77	4.37	6.14
	VV	1.87	4.46	6.33
	HA	1.86	3.54	5.40
Dichromats				
Deuteranopes	LH	6.45	6.37	6.41
	DA	5.99	6.23	6.11
	SH	7.05	6.30	6.68
Protanopes	PR	6.26	6.25	6.26
	MP	6.73	6.28	6.51
	KG	6.51	5.91	6.21

Trichromats 5.99 ± 0.17 cones.
Deuteranopes 6.40 ± 0.20 cones.
Protanopes 6.33 ± 0.11 cones.

of dichromat LH for a test of the same size and of wavelengths either 520 or 640 nm. These two data sets are best fit by theoretical functions which correspond to values of 14.7 and 14.5, respectively, as the total numbers of cones contributing to detection. These results show that under conditions wherein both L and M cones of the trichromat can contribute to detection of the test, our methods produce an estimate of total cone density for the trichromat which is similar to the estimate of total cone density for the dichromat.

DISCUSSION

The evidence that the dichromatic foveal mosaic is as densely packed as that of the trichromat is given by our estimates that the number of cones underlying the retinal image of the test of one min in diameter is 6.33 for our group of protanopes, 6.40 for our group of deuteranopes, and 5.99 for our group of trichromats. Nondirectional t-tests revealed no significant differences between the means of the three groups of observers ($P > 0.14$) or between the means of the six dichromatic observers and the six trichromatic observers ($P > 0.05$). Thus, on the basis of the nondirectional t-tests, the differences among the groups must be considered to be within the range of sampling error. A directional t-test of the differences between the means of trichromatic and dichromatic groups indicated that the mean foveal cone density of the dichromatic observers is significantly greater than that of the trichromatic observers ($P < 0.05$). Overall the results support the conclusion that the density of cones in the dichromatic fovea centralis is comparable to (and perhaps greater than) the density of cones in the trichromatic fovea centralis. Furthermore, there is no indication in our results that, as compared to trichromats, individual dichromats may have a lower density of cones in fovea centralis, since every dichromat exceeded the mean value obtained for trichromats.

For detection of these tiny tests of 1 min in visual angle, under the assumptions of our model, the results are consistent with the requirement of at least 6 quanta absorbed per cone in the human dichromatic fovea centralis. This estimate is close to the values obtained for the human trichromat in a number of studies based on the detection of small spots of light. Marriott (1963) estimated, for 9 observers, a value of at least 5 quanta absorbed per cone; Vimal, Pokorny, Smith and Shevell (1989) obtained an estimate of between 5–7 quanta per cone for 2 observers; Cicerone and Nerger (1989) estimated a value of at least 6 quanta per cone from the results of 6 observers. The estimates of Vimal et al. (1989) and Cicerone and Nerger (1989) were made separately for the M and the L cones in the trichromatic fovea. That the results for the protanopes as well as the deuteranopes in this study was consistent with the same value of the minimum number of quanta absorbed per cone, lends credence to the idea that the functioning of the M and L cones do not differ in this aspect.

It should be noted that our model and its associated assumptions (Cicerone & Nerger, 1989) from which we derived estimates of the number of cones contributing to the detection of our test are not strictly required for our conclusions. The results of Fig. 4 provide a qualitative answer to our question, in that if the L cones, as well as the pigment erythrolabe, were missing in the protanope, then his detection function should match that of the trichromat measured under M cone isolation conditions. A similar argument holds for the deuteranope. Instead, as compared to the trichromat, all protanopes and deuteranopes yielded detection functions with steeper slopes, indicating a larger

number of cones filled with chlorolabe in the protanopic eye as compared to the trichromat, and a larger number of cones filled with erythrolabe in the deuteranopic eye as compared to the trichromat. The application of curve-fitting procedures allowed us to quantitatively estimate the numbers of cones contributing to detection (Table 1), and we conclude from these estimates that the total numbers of cones in fovea centralis of dichromats match that of color normal trichromats.

Comparisons to other estimates of foveal cone density

An independent estimate of the expected number of cones underlying the stimulus can be obtained from histological measurements of the foveal cone density given by Osterberg (1935), Miller (1979), Ahnelt et al. (1987), and Curcio et al. (1987). The center-to-center spacing among the cones (d_{cc}) consistent with these anatomical studies was calculated using the standard equation:

$$d_{cc} = (1000/\sqrt{N})(2/\sqrt{3})^{0.5};$$

where N equals the cone density in cones per square millimeter and d_{cc} is in micrometers. A factor of 0.291 millimeters per degree of visual angle and an axial focal length of 16.667 were assumed in order to convert the retinal distances to angular measurements. The conversion further assumed that the packing of photoreceptors form a regular triangular array. The calculations yielded a mean value of 0.55 min arc as the center-to-center separation among cones in the fovea centralis. In order to estimate the number of cones illuminated by our test spot of one min in diameter, we calculated the retinal image of our test by applying the standard optical spread function of the human eye (Campbell & Gubisch, 1966). The effective gathering area of the M and L cones was assumed to be half the diameter of the cone inner segment (MacLeod, Williams & Makous, 1985). Based upon all the foregoing considerations, we calculated that from 5 to 7 cones would be expected to be illuminated by the retinal image of the test of 1 min in visual angle falling upon the anatomically defined mosaic. The estimates obtained from our procedures for each of the 6 dichromatic and 6 trichromatic observers (Table 1) all fall within this anatomically defined range. We also calculated that 14–16 cones should underlie the retinal image of our test of 2 min in visual angle. Our measurements indicate values within this range (Fig. 5). This close agreement with the anatomical results adds validity to our model and to our estimates of cone densities in human fovea centralis.

We can also make a comparison of our measurements to the cone mosaic recently defined by Williams (1988), who used a psychophysical procedure to estimate the density of cones in and near the human fovea. Williams' (1988) estimates of mean cone spacing in the foveae centralis of eight human eyes can be converted to an estimate of 5.68 as the number of cones which are expected to be illuminated by our test of diameter 1 min in visual angle. As shown in Table 1, the mean values obtained from our estimates were 5.99 (SEM 0.17) for 6 trichromats, 6.40 (SEM 0.20) for 3 deuteranopes, and 6.33 (SEM 0.11) for 3 protanopes. The mean value for all 12 observers was 6.18 (SEM 0.10). Our estimates are reasonably close to what is expected on the basis of Williams' (1988) measurements.

Models of dichromacy

Our results favor a general model for dichromacy which specifies that although the dichromatic fovea lacks one of the three cone photopigments, it retains the full complement of numbers of cones. On the basis of color matches (Maxwell, 1855; Pitt, 1944; Wright, 1946) selective adaptation (Wald, 1964, 1966) and densitometric measurements (Rushton, 1963, 1965; Alpern & Wake, 1977), it is generally acknowledged that dichromats lack one of the three cone photopigments present in the trichromatic fovea. Our results show identical detection functions measured for the dichromatic eye under two conditions, one designed to isolate L cones and the other to isolate M cones in the trichromatic eye (Fig. 2). Given the earlier studies cited above, our result is just what is expected on the basis of the presence of only one cone pigment, either erythrolabe or chlorolabe, in the dichromatic eye, in the wavelength range spanned by these two cone pigments in the color normal trichromat.

For the sake of completeness, it should be noted that a fusion model of dichromacy, which postulates that all three cone types are present in the dichromatic eye, but that the M and L pathways are fused, is not supported by our results, since such a model would not predict the results shown in Figs 2–4. Chromatic adaptation would be expected to produce selective desensitization of one of the two cone types in

the fused pathway. Thus, even with a full complement of numbers of cones, under chromatic adaptation a fusion model would predict a match of the protanopic detection function with that of the trichromat under *M* cone isolation, and similarly, a match of the deuteranopic function to that of the trichromat under *L* cone isolation.

There are a number of models, differing in the ways in which postreceptoral processing of signals from the cones may take place, which are consistent with the conclusions of the present study. The results of the present study are limited in that, on their own, they do not allow an evaluation of the nature of such postreceptoral process involved in dichromacy. In particular, consistent with our finding that the numerosity of cones in the fovea of the dichromat equals that in the trichromat, are two possible ways in which the signals of cones can be combined at the red/green opponent site. One possibility is that the neural connections into the color opponent site are as for the color normal trichromat. In this scheme (often called a replacement model) the only difference between dichromats and trichromats is that in protanopes the pigment chlorolabe fills both *M* and *L* cones, and in deuteranopes erythrolabe fills both *M* and *L* cones. Although *M* and *L* cones are filled with the same pigment, they do not have the same neural connections into the opponent site. Instead, the cones retain their neural connections as for the trichromat, *M* cones contributing to greenness and *L* cones contributing to redness. A second possibility specifies that all cones filled with the same pigment have the same connections. This model is often called a neural loss model in that one set of neural connections is lost. Thus in the protanope, all cones filled with chlorolabe have the same connections, which are akin to those made by *M* cones in the trichromat, and the connections which would be made by erythrolabe-filled *L* cones in the trichromat are absent. According to this model, an analogous condition holds for the deuteranope. In order to distinguish between the replacement and the neural loss models of neural connectivity, we note that a previous study (Cicerone, Nagy & Nerger, 1987) evaluated equilibrium hue judgements of dichromats to conclude that the neural loss model is favored over the replacement model. Thus in combination, the evidence from this study and that of Cicerone et al. (1987) allow us to favor a model for dichromacy in which a pigment is lost, but the full complement of numbers of cones is retained, and which further specifies that the neural connections made by the cones correspond to the pigment which they contain.

These conclusions are generally, although not completely, consistent with recent evidence showing that protanopia and deuteranopia can each be identified with distinct alterations in the genes encoding erythrolabe and chlorolabe (Nathans, Piantanida, Eddy, Shows & Hogness, 1986a; Nathans, Thomas & Hogness, 1986b). The genotypes of dichromats in this sample produced, within each main classification as protanope or deuteranope, a number of different subgroupings of genotypes involving combinations of wild-type and hybrid X-linked color vision genes. Although the phenotypes of the individuals in the studies of Nathans et al. (1986a, b) were not completely determined, the possibility that these different genotypes can be expressed as diverse forms of protanopia or deuteranopia cannot be discounted. As noted above, in contrast to the large diversity in classifications of genotypes among individuals from the results of molecular biology, we find a more restricted range of classification of dichromats according to our psychophysical results.

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