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EQUILIBRIUM HUE JUDGEMENTS OF DICHROMATS

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Abstract—It is generally held that protanopes and deuteranopes see only regions of blues and yellows in the visible spectrum, with an achromatic point, called the neutral point, separating these regions. Considerations of a zone model of color vision for the dichromatic observer led us to predict that a reduced form of red/green discrimination would allow equilibrium blue judgements to be made by protanopes. We show that protanopes can make equilibrium blue determinations with as much reliability as they make neutral point settings. Our results indicate that protanopes but not deuteranopes are able to rely on a reduced form of red/green discrimination in the short wavelength part of the spectrum. Protanopes describe wavelengths longer than the neutral point as yellow. Between the neutral point and equilibrium blue, different wavelengths are described as having varying aspects of blue and green; and short of equilibrium blue they appear reddish blue. For deuteranopes, the spectrum longer than the neutral point appears yellow, and short of it, blue. The results of our experiments showing that the protanopic equilibrium blue is invariant with intensity variations, as it is in the trichromat, add support to the idea of a reduced form of red/green discrimination for protanopes. Our results also allow the evaluation of various models of protanopia.

Dichromacy Color appearance Red/green chromatic pathway

INTRODUCTION

Protanopes and deuteranopes are believed to be incapable of making foveal small-field, red versus green judgements. Indeed, these individuals are conventionally called "red-green blind dichromats," and color appearance for them is assumed to vary only along a dimension analogous to what is the yellow versus blue axis for the normal trichromatic observer (Dalton, 1798; Judd, 1948; Jameson and Hurvich, 1955). That this need not necessarily be so can be appreciated by considering the model shown in Fig. 1. In order to make clear the distinctions among the different cone pigments, the different cone types and their associated neural connections, and the perceptual qualities of redness and greenness, we use the following separate designations. The short wavelength absorbing pigment (α) normally resides in the S cones, the middle wavelength absorbing pigment (β) in the M cones, and the long wavelength absorbing pigment (γ) in the L cones. In our model redness (R) is coded by combining the L and S cone responses, and this is pitted against the M cone response which codes greenness (G). On the basis of color matching data (Maxwell, 1855; Pitt, 1944; Wright, 1946) and densitometric measurements (Rushton, 1963, 1965; Alpern and Wake, 1977), it is generally acknowledged that dichromats lack one of the three pigments present in the trichromatic fovea. This is further supported by recent evidence showing that protanopia and deuteranopia can each be identified with distinct alterations in the genes encoding the γ and β pigments (Nathans *et al.*, 1986). What remains controversial is the exact nature of the neural connections which form the basis of color coding in the dichromatic eye. To begin, consider the simple model for protanopia outlined in Fig. 1. If protanopes lack the L-cone system, including the γ pigment and the neural connections made by the L cones, but all else remains as for the trichromat, then we can make a prediction that red versus green opponency should be preserved in the short wavelength part of the spectrum. Furthermore, protanopes should be able to make judgements of equilibrium blue, a color which is uniquely blue in the sense that it is neither reddish nor greenish. On the other hand (as illustrated at the bottom of Fig. 1), for deuteranopes who lack the M cone system, since S cones as well as L cones

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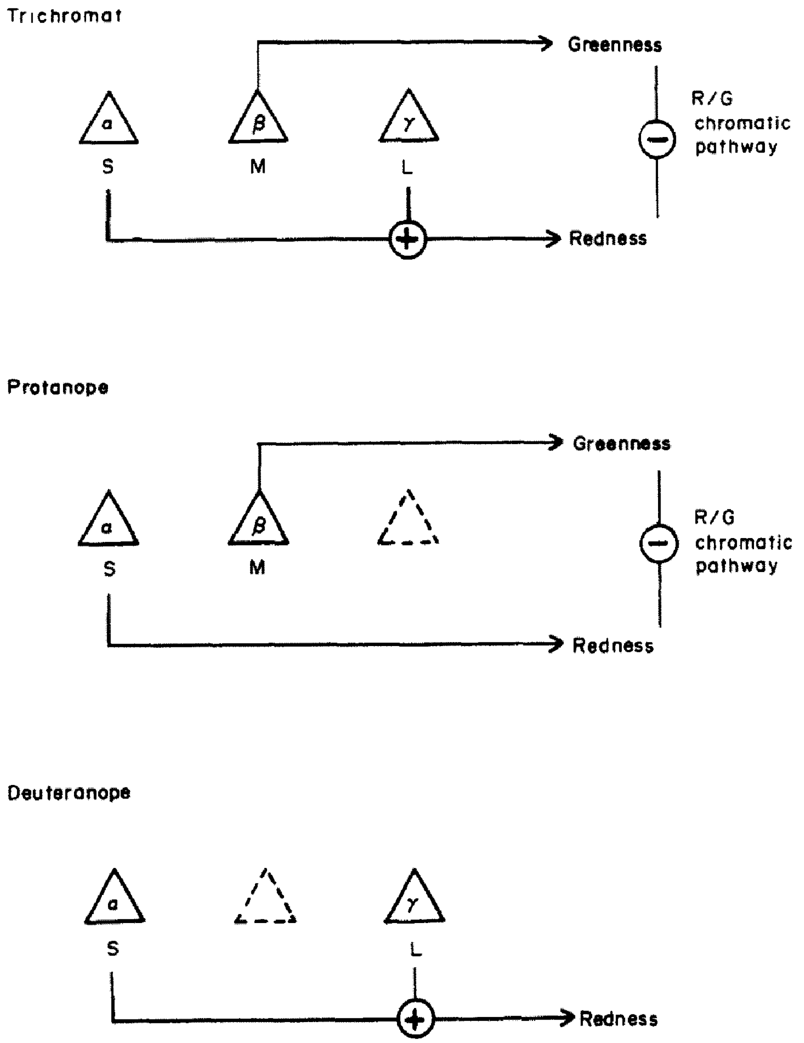

Fig. 1. Shown at the top is a model for the red/green opponent chromatic pathway in the trichromat. The short wavelength absorbing pigment (α) resides in the S cones, the middle wavelength absorbing pigment (β) in the M cones, and the long wavelength absorbing pigment (γ) in the L cones. L-cone and S-cone responses contribute to the perception of redness (R) and M cone responses contribute to greenness (G). Dichromacy is represented as a reduced form of trichromacy, with protanopes lacking the L cone system and deuteranopes lacking the M cone system. See text for details and predictions made by this model.

contribute to redness, all short wavelengths have the same polarity, and red versus green judgements should prove impossible.

In this paper we report experimental tests of these ideas. As we anticipated, protanopes, but not deuteranopes, are capable of making red versus green judgements in the short wavelength part of the spectrum. They do so with as much reliability as they make neutral point judgements. Under the assumption that dichromacy represents a reduced form of trichromacy, then in as much as our results indicate that S cones contribute to redness in the dichromat, they also support a model wherein S cones as well as L cones contribute to the perception of redness in the normal trichromat. We also used our results to evaluate different models of protanopia.

METHODS

Subjects

Subjects were color normal trichromats, and six protanopes and four deuteranopes diagnosed to be dichromatic on the basis of anomaloscope matches, neutral point matches to tungsten white and small field color matches. We tested one protanope and one deuteranope with large as well as small field matches, and these two were dichromatic even with large field tests.

Stimulus and apparatus

The stimulus, presented in Maxwellian view, was a 1°, centrally fixated test light which flashed 0.5 sec every 2.5 sec and which varied between 30 and 1000 td in retinal illumination.

All channels of the standard Maxwellian view apparatus had a common source, a 6 V tungsten iodide lamp. Light from one channel was passed through a monochromator (Instruments SA, H-10). Light from two other channels could be combined in varying proportions with the aid of two polarizers (Polaroid HN22). A fourth channel provided the fixation lights. The size of the Maxwellian image was 1 mm by 2 mm.

The observers were aligned with the aid of a dental impression bite bar which was mounted on a stand that allowed adjustments in three dimensions.

Calibrations

An EG & G radiometer/photometer (Model 450) was used for measurements of retinal illumination and for calibrations of the neutral density wedges and filters.

Procedures

Subjects viewed monochromatic lights which varied in retinal illumination over approximately a factor of 30. The subject's task was to use color names to describe lights which were presented in a sequence of randomized staircases which were interleaved among the different intensity levels. Protanopes spontaneously used terms such as "purple", "violet", "green", or "yellow" to describe lights between 400 and 700 nm. Deuteranopes used the terms "dark blue", "blue", or "yellow" to describe this same range of colors.

In a second procedure (used for the experiments of Fig. 3), subjects controlled the relative amounts of 430 and 520 nm lights presented in combination. In the case of a neutral point setting, subjects were asked to obtain a color which was most nearly white, with as little aspect of any other color as possible. For equilibrium blue settings, the subject's task was to achieve a blue with as little aspect of any other color as possible.

RESULTS

Equilibrium blue judgements of protanopes

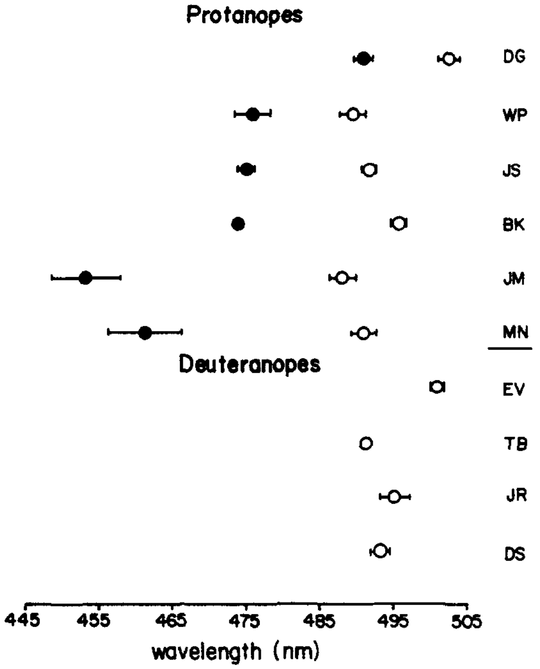

Fig. 2. Neutral point (open symbols) determinations for six protanopes and four deuteranopes and equilibrium blue (solid symbols) determinations for the six protanopes are shown. Error bars mark ± 1 SEM computed as day-to-day variability.

Neutral point and equilibrium blue determinations were made for six protanopes and four deuteranopes. The results for a 10 td test light are shown in Fig. 2. Protanopes made equilibrium blue judgements with as much reliability as they made neutral point settings. For each of the six protanopes the neutral point settings were at longer wavelengths than the equilibrium blue determinations by 11.8, 14.3, 18.5, 19.9, 29 and 29.6 nm.

The neutral point settings for the four deuteranopes are also shown in Fig. 2. The entire spectrum of wavelengths shorter than the neutral point was judged as unvaryingly blue or dark blue, and so an equilibrium blue could not be determined for deuteranopes.

Subject D.G., who was the only female in our pool of subjects, appears to be different from the rest of the protanopes as a group. Excluding D.G.'s results, the mean value of the neutral points measured for the protanopes was 490.6 ± 1.5 nm and for deuteranopes the mean value was 495.2 ± 2.07 nm.

Mixtures of violet and green lights

Our next experiment was designed to test the reliability of the protanopic equilibrium blue determinations. Subjects were instructed to attain an equilibrium blue by varying the relative amounts of 430 and 520 nm lights in a mixture. If one were to vary the luminance of the 520 nm

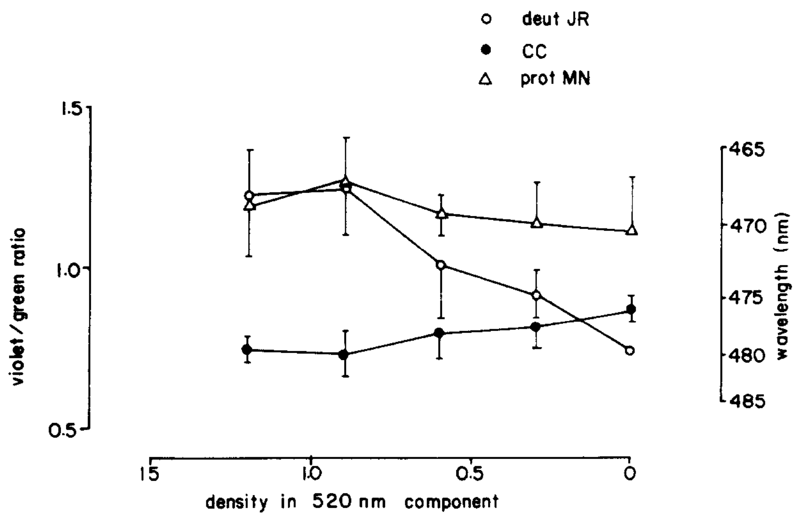

Fig. 3. The ratio of violet (430 nm) to green (520 nm) lights in a mixture which produced equilibrium blue is plotted as a function of the density placed in the 520 nm component. A fixed violet to green ratio corresponds to a particular monochromatic wavelength. The trichromat (solid circles) and protanope (open triangles) maintain a constant violet to green ratio, but the deuteranope (open circles) does not.

component, a reliable subject, who is basing his judgements on the amounts of redness versus greenness in the stimulus, should make a compensatory change in his setting for equilibrium blue so that the ratio of violet to green light remains unchanged. Figure 3 shows results of just such an experiment for a normal trichromat (C.C.) one of our protanopes (M.N.) and a deuteranope (J.R.). Deuteranope J.R. was instructed to do as well as he could in determining a mixture which was blue with as little aspect of any other color as possible. The abscissa represents the density placed in the 520 nm component. The ordinate scale at the left represents the ratio of the violet (430 nm) to green (520 nm) components. The ordinate on the right represents the dominant wavelengths (calculated from the CIE diagram) of the mixtures. Consistent settings would be represented by a horizontal line (constant violet to green ratio). The protanope and the normal trichromat produced results which show a maintenance of the ratio, whereas the deuteranope does not. As the luminance of the 520 component is increased, deuteranope J.R. does not compensate by increasing the amount of violet light he chooses to add to the mixture. Thus, although J.R. apparently adopted a procedure which gives fairly consistent between day results, his settings are clearly not based on the amounts of redness or greenness in the stimulus.

All of our protanopes passed this test which checks the reliability of their equilibrium blue settings. When the same test was applied to neutral point settings, all deuteranopes and protanopes made compensatory settings.

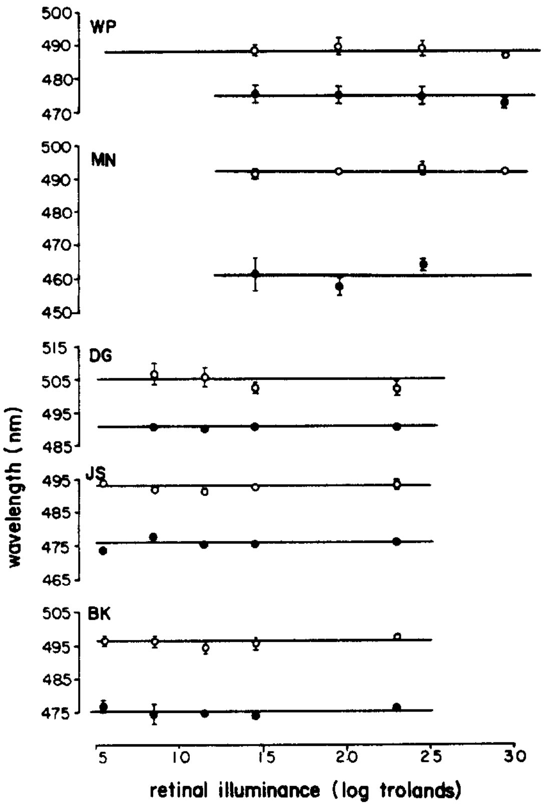

Fig. 4. Equilibrium blue (solid symbols) and neutral point (open symbols) determinations as a function of retinal illumination varying over a 30-fold range are shown for five protanopes.

Intensity invariance of equilibrium blue

If red/green opponency in protanopes is a reduced form of the red/green opponent code in normal trichromats, equilibrium blue judgements should be stable under intensity variations. The importance of this test has been pointed out by Krantz (1975) who showed that if the set of red/green equilibrium colors is closed under linear color mixture operations (that is, additive mixture and scalar multiplication), then a linear function of the color matching functions will describe the red/green opponent process. Larimer *et al.* (1974) among others, have provided evidence that in the normal trichromat, this is indeed the case. Figure 4 shows the results of our measurements on five of our original six protanopes. The sixth protanope left the experiment before we could complete these measurements.

Neutral point determinations as well as equilibrium blue judgements were made. As has been previously shown by Knoblauch and Wooten (1982), neutral point settings are invariant with intensity. Also shown in this figure is that equilibrium blue settings are invariant with intensity.

DISCUSSION

Previous reports in the literature have pointed to the possibility of residual red/green discrimination in the long-wavelength part of the spectrum for observers who appear to be dichromatic by standard tests (Scheibner and Boynton, 1968; Smith and Pokorny, 1977; Nagy, 1980, 1981; Breton and Cowan, 1981). These previous studies used large test fields (3–8 deg) which necessarily included extrafoveal areas. We emphasize here, that our results were obtained with small, foveal fields. All our subjects were dichromatic as determined by standard tests of color vision, including small field color matches. Contrary to other studies (cited above) which point to the possibility that rods or a third cone pigment may be involved in large field color discriminations made by dichromats, our screening procedures and experimental results show no evidence of the involvement of more than two pigments for the small, foveal fields we employ. Thus our results do not challenge the basic idea that there are only two pigments in the dichromatic fovea. Instead, our results can be used to evaluate different models of the neural connections which form the opponent chromatic pathways.

It is generally held that protanopes and deuteranopes see only regions of blues and yellows in the visible spectrum, with an achromatic point, called the neutral point, separating these regions. Considerations of a zone model of color vision for the dichromatic observer (see Fig. 1) led us to predict that a reduced form of red/green discrimination would allow equilibrium blue judgements to be made by protanopes. We have shown that protanopes can make equilibrium blue determinations with as much reliability as they make neutral point settings. Our results indicate that protanopes but not deuteranopes are able to rely on a reduced form of red/green discrimination in the short wavelength part of the spectrum. Protanopes describe wavelengths longer than the neutral point as yellow. Between the neutral point and equilibrium blue, different wavelengths are described as having varying aspects of blue and green; and short of equilibrium blue they appear reddish blue. For deuteranopes, the spectrum longer than the neutral point appears yellow, and short of it, blue. The results of our experiments showing that the protanopic equilibrium blue is invariant with intensity variations, as it is in the trichromat, further supports the idea of a reduced form of red/green discrimination for protanopes.

These results are consistent with a model for the red/green chromatic pathway in protanopia wherein the S cones contribute to redness and the M cones to greenness. For the deuteranope S and L cone types both contribute to redness. Inasmuch as our results are consistent with a model wherein the S cones contribute to redness in the dichromat, the results also support such a model of trichromatic color vision. Our results are consistent with previous studies showing S cone influence on the red/green pathway in trichromats (Jameson and Hurvich, 1968; Cicerone *et al.*, 1975; Ingling *et al.*, 1978; Wooten and Werner, 1979).

It should be noted that none of these results imply a tridimensional color space for protanopes. One scheme that is consistent with our results and the essential two-dimensional nature of protanopic color vision is the following: Luminance is coded directly as the contribution from the M cone system. The yellow/blue code involves a weighted difference between M and S cone quantum catches and the red/green code involves another weighted difference. Thus

$$\text{Luminance:} \quad M$$

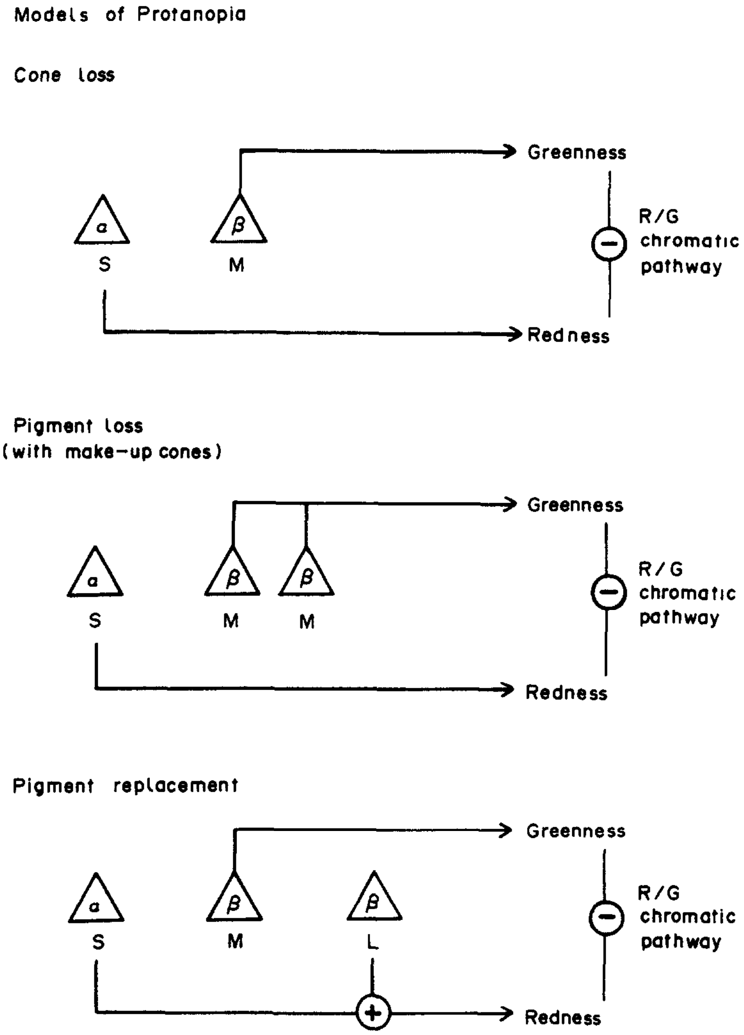

Fig. 5. Three models of protanopia are shown. See text for the explanations of the differences among them and for the predicted locations of equilibrium blue points.

Yellow/Blue: $k_1M - S$

Red/Green: $S - k_2M$

where k_1 and k_2 are weighting coefficients. The neutral point is the wavelength λ_1 such that

$$k_1M(\lambda_1) - S(\lambda_1) = 0.$$

The equilibrium blue point is the wavelength λ_2 such that

$$S(\lambda_2) - k_2M(\lambda_2) = 0.$$

It is clear that these three color codes are not independent and also that λ_1 is distinct from λ_2 unless $k_1 = k_2$. The results shown in Fig. 2 imply that k_1 and k_2 are not identical.

An interesting consequence of this formulation is the prediction that the neutral point measured for a protanope may appear green. The neutral point can be considered as the wavelength for which the yellow/blue system is in equilibrium, or as expressed above, the yellow/blue code has zero value. Since the red/green system is not in equilibrium at this same wavelength, but at a shorter wavelength, the equations predict that the neutral point should appear green. How green it appears depends on the weighting factor k_2 and the strength of the residual red/green system in the protanope. As noted earlier, in the region near the neutral point protanopes use the color name green, but they tend to describe wavelengths longer than the neutral point as yellow. This is an indication that the red/green system is indeed weak and is dominated by the yellow/blue system in determining the perception of wavelengths longer than the neutral point.

Our results appear to run counter to those of

Romeskie and Yager (1978) who measured chromatic opponent response functions for one protanope and one deuteranope. Using cancellation wavelengths of 470 and 600 nm, they determined that the two dichromats in their study were always able to adjust the mixture of tests and cancellation stimuli so that the mixture appeared "white", with no residual hue component. They further determined that the best fits to their chromatic opponent response data were obtained by assuming that the β pigment's peak sensitivity was 540 nm and that the γ pigment's peak was 557 nm. We note that the estimate for the γ pigment peak obtained from their deuteranope's results is close to the microspectrophotometric estimate of 558.4 ± 5.2 nm recently obtained for single human L cones (Bowmaker and Dartnall, 1980). However, Romeski and Yager's estimate of the β pigment peak (540 nm) which is derived from their protanope's data is not comparably close to Bowmaker and Dartnall's estimate of 530.8 ± 3.5 nm for M cones. It is difficult to evaluate this rather large difference of roughly 10 nm since Romeskie and Yager's study involved only one protanope; however, the difference would appear to be outside the range of individual variation among protanopes as measured by psychophysical techniques (Bastian, 1976; Alpern, 1981; MacLeod and Webster, 1983). We can only suggest that this discrepancy may indicate that the cancellation procedure did not succeed in reducing the spectral wavelengths to "white" as successfully for the protanope as it did for the deuteranope. It is also possible that Romeski and Yager's procedures which differed from ours in employing rather long test exposure durations of seven seconds and the method of adjustment, may not have been as sensitive as our procedures in allowing the measurement of small differences in color appearance. It is well known that small differences in color appearance fade with long exposure durations in both normal and color deficient observers (McCree, 1960; Clowes, 1962; Cohen and Greenbaum, 1982).

Finally, we can analyze the results of our experiments in terms of various models of protanopia. These models are illustrated in Fig. 5. For the model which we call cone loss, the L cone system is absent. This model predicts that the equilibrium blue wavelength chosen by a protanope should be shorter than or equal to the wavelength chosen by the trichromat, in order to compensate for the lack of a positive L cone signal contributing to redness. In the model called pigment loss, there is a full complement of cones. Some cones are filled with short- and others with middle-wavelength absorbing pigment. The neural circuitry for all cones filled with middle-wavelength absorbing pigment is the same, thus enhancing the strength of the greenness signal. Therefore, this model predicts a protanopic equilibrium blue which lies at shorter wavelengths than that of the normal trichromat. For a pigment replacement model of protanopia, the L cones, normally filled with long-wavelength absorbing pigment (γ) are now filled with middle-wavelength absorbing pigment (β). Assuming no neural changes so that L cones still contribute to the red/green code with a polarity opposite to M cones, this results in reduced strength for the greenness signal. The prediction in this case is that the equilibrium blue wavelength for protanopes should be found at longer wavelengths than the trichromat's equilibrium blue.

Our results can be compared to the predictions of these models. Shown in Fig. 6 is the MacLeod–Boynton (1978) chromaticity diagram in which, for stimuli of equal luminance, excitation of each cone type is represented by a linear scale. Represented along the abscissa is a

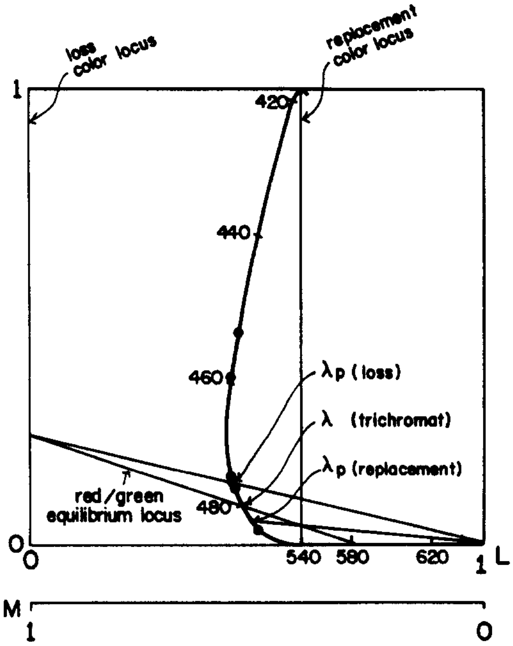

Fig. 6. Equilibrium blue determinations (solid circles) obtained from our six protanopes are displayed in the MacLeod–Boynton chromaticity diagram. Five of six protanopes chose equilibrium blue points which are located at wavelengths shorter than the color normal trichromatic observer's equilibrium blue point.

scale proportional to the excitation of long-wavelength absorbing cones, here labeled L with values increasing rightward. Also along the abscissa, but with values increasing leftward is the scale proportional to middle-wavelength cone excitation, labeled M. The ordinate (S) represents excitation in the short-wavelength absorbing cones and increases upward. The heavy curve marks the spectrum locus in this color space. Protanopic confusion lines in this diagram emanate from the lower right hand corner. Either loss model, cone loss *or* pigment loss with make-up cones, places the line representing the color locus for protanopes along the ordinate. A pigment replacement model yields a vertical line whose exact placement is determined by the particular assumptions one makes about the relative heights of the β and γ absorption spectra; but all reasonable assumptions lead to the prediction that the protanope's equilibrium blue should be at a wavelength longer than the trichromat's. Now, the locus of points describing colors in red/green equilibrium for the normal trichromat is shown as the line connecting trichromatic equilibrium blue and equilibrium yellow. This line intersects the loss color locus as well as the replacement color locus. To obtain the spectral wavelength predicted to be equilibrium blue for protanopes, we simply note the intersection locus. λ indicates the trichromatic equilibrium blue, and λ_p the predicted protanopic equilibrium blue. The closed circles show the mapping of the equilibrium blue wavelengths measured for our six protanopes in this diagram. Five of six determinations all lie in the direction predicted by the loss models, that is they all lie at wavelengths shorter than the normal trichromat's equilibrium blue. Thus these results tend to discredit a pigment replacement model for protanopia.

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