Large-field trichromacy in protanopes and deuteranopes

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Protanopes and deuteranopes do not accept the classical dichromatic matches when field size extends to 8° visual angle. Their unique matches of spectral yellow to a mixture of red and green are then mediated by the photoreceptors of small-field dichromacy interacting with a photoreceptor with the spectral sensitivity of rhodopsin. Our data suggest that large-field trichromacy is a general feature of protanopia and deuteranopia.

Many protanopes and deuteranopes insist that they enjoy a unique percept for red light. Color theorists doubt this claim since protanopes and deuteranopes are dichromats: they can match all spectral colors using suitable mixtures of two primary colors. Protanopes and deuteranopes are thought to see the spectrum as shades of blue and yellow separated by neutral grays in the spectral region corresponding to 500 nm.1-3 In an anomaloscope with 545 nm (green) and 670 nm (red) primaries, protanopes and deuteranopes behave as monochromats; they match either the 545 nm primary, or the 670 nm primary, or any mixture of these primaries to spectral yellow. In fact, dichromats will match spectral green to spectral red. The basic dichromatic performance of protanopes and deuteranopes in color matching has been confirmed for foveal fields in many laboratories.1,4,5 Thus, when a dichromat claims to see “red,” he is greeted with skepticism and treated to explanations designed to annul his “red” perception.4

However, occasional studies suggest that by enlarging the field to include parafoveal regions, dichromats may encounter an added dimension of color perception.6-11 Nagel7 noted that although he was a deuteranope with a field of less than 2° extent, he became trichromatic with a field of 10°. Nagel8 confirmed these findings on 30 other dichromats. Based on the appearance of red-green color-mixture fields, Nagel9 concluded that he was a deuteranomalous trichromat with a large field. His suggestion, however, was not based on a study of metameric color matches. Jaeger and Kroker10 found that two of seven deuteranopes and six of nine protanopes would not accept a neutral point match for a 22° field. They called these observers incomplete dichromats and followed Nagel10 in suggesting that their color vision was that of the corresponding anomalous trichromat. Boynton and Scheinber11 and Scheinber and Boynton11 found that some of their dichromats had difficulty setting a neutral point match with a 3° field. These data, taken with some color naming data, led them to the hypothesis that such observers had residual red-green discrimination mediated by normal cone photopigments; but they mention rod intrusion as an alternative. Boynton and Scheinber11 suggested that the ability to make red-green discriminations might be a general feature of dichromacy.

Thus the studies6-11 show little agreement on the universality of the phenomenon, nor do they indicate how such an added dimension of discrimination might be mediated. Further, there have been no studies of the large-field color matches made by dichromats. In this paper, we examine dichromatic coefficients and red-green matches made by protanopes and deuteranopes with field sizes of 1°, 2°, 4°, and 8° to examine the different hypotheses8-11 and to see if the matches reveal any basis for the dichromat’s claim of a distinct chromatic sensory perception of long-wavelength stimuli.

METHODS

Equipment. A Moreland Universal Anomaloscope12 was used. Modifications of the instrument have been described previously.13 The left half-field was filled by a single nearly monochromatic beam (test field), the right half-field by an additive mixture of two nearly monochromatic beams, the primaries, P1 and P3 (mixture field). The interference filters used for this study were from various manufacturers. Wavelength of peak transmission and half-height bandwidth were measured in the anomaloscope with a calibrated laboratory-constructed photoelectric spectroradiometer. Half-height bandwidths ranged from 7 to 14 nm. Field stops provided circular fields subtending 1°, 2°, 4°, and 8°. An additional field stop provided an 8° circular aperture with the central 4° blackened out.

Procedure. The anomaloscope was used in a manner essentially identical to that of the Nagel anomaloscope.14 The spectral test field was variable in luminance; the primary mixture field had variable proportions of P1 and P3. The field was freely viewed; each observer used his preferred eye. Room illumination was dimmed, and the observers adapted to the field illumination. Observers were cautioned not to stare continuously at the field but rather to use a glance technique in which they looked away every 10–12 s. When the 8° annular stop was used, observers were instructed to fixate the center of the black circle.

Observers. We advertised locally for color-defective observers. Observers were accepted as dichromats if on the Nagel anomaloscope they matched in hue 670 to 589 nm and 545 to 589 nm, and also if they made a neutral point match for the 2° field between a 7000 K white and a mixture of 450 and 650 nm. Eighteen of the individuals responding to our advertisement were classified as dichromats by this method.

EXPERIMENT 1: ANOMALOSCOPE SCREENING WITH VARYING FIELD SIZE

Our first attention was directed to the discrepancy between Nagel9 and Jaeger and Kroker10 as to how many dichromats would refuse a dichromatic large-field...
TABLE I. Rayleigh matches accepted (✓) or rejected (x) by deuteranopes and protanopes as a function of field size.

<table>
<thead>
<tr>
<th></th>
<th>Field size</th>
<th>Field size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1°</td>
<td>2°</td>
</tr>
<tr>
<td>589 + 670 nm</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>589 + 545 nm</td>
<td>✓</td>
<td>✓</td>
</tr>
</tbody>
</table>

Deuteranope

DK        ✓  x  x  ✓  ✓  x
M M        ✓  ✓  x  ✓  ✓  x
JK        ✓  x  x  ✓  ✓  x
KK        ✓  x  x  ✓  ✓  x
DR        ✓  ✓  x  ✓  ✓  x
MB        ✓  ✓  x  ✓  ✓  x
LB        ✓  x  x  ✓  ✓  x
JD        ✓  ✓  x  ✓  ✓  x
KG        ✓  x  x  ✓  ✓  x
CM        ✓  ✓  ✓  ✓  ✓  x
TR        ✓  ✓  ✓  ✓  ✓  x

Protanopes

CB        ✓  ✓  x  ✓  ✓  x
SY        ✓  ✓  x  ✓  ✓  x
DP        ✓  ✓  x  ✓  ✓  x
DS        ✓  ✓  x  ✓  ✓  x
JM        ✓  x  x  ✓  ✓  x
DV        ✓  ✓  x  ✓  ✓  x
MG        ✓  ✓  x  ✓  ✓  x

match. The purpose of the first experiment was to check how many of the 18 dichromats would continue to accept a match of 589 to 670 nm or 589 to 545 nm as the field size was increased to 8°.

Procedure. We used primaries of 545 and 670 nm in the mixture field and a 589 nm light in the test field. The field luminance was 5 candles/m². For each circular stop, 11 deuteranopes and 7 protanopes were asked to match (i) the 545 nm primary, and (ii) the 670 nm primary to the 589 nm light by adjusting the luminance of the 589 nm test field. In addition, two protanopes, SY and CB, and two deuteranopes, DK and MM, were asked to make the matches using the 8° annular stop.

Results and discussion. All observers made both matches with the 1° field (Table I). As the field size increased, more observers reported that they did not have an exact color match. They were more likely to refuse the 589–670 nm condition than the 589–545 nm condition. With the 8° field, only two 589–545 nm matches were accepted. The observers commented spontaneously that the fields appeared increasingly different in color as field size increased. Since all eighteen dichromats were unable to make 8° matches, the results show that this is a general phenomenon of dichromatic color vision, as postulated by Nagel.

The annular field stop was used to evaluate the possibility that retinal inhomogeneity was the source of the match refusal. With the annular field stop, protanope CB and deuteranope MM accepted the 589–545 match, but not the 589–670 match. Protanope SY and deuteranope DK rejected both matches. These data suggest that retinal inhomogeneity between foveal and parafoveal regions was not the cause of match rejection.

Failure to accept dichromatic matches, however, might be explained by postulating increased sensitivity to saturation differences of the spectral lights. An interpretation of dichromatic color-mixture data is that a wavelength which matches a mixture of two spectral primaries is less saturated in appearance than either spectral primary itself. Color matching data using 450 and 650 nm spectral primaries show that test wavelengths above 540 nm are matched to mixtures containing a high proportion of 650 nm primary. The proportion is near 0.98 at 540 nm, approaching unity at 650 nm. These data suggest a very slowly increasing saturation of long-wavelength lights. Since the precision of color matching improves with an increase in field size, failures to accept a match of 589 to 670 nm might be attributed to the dichromat's ability to discriminate a very small saturation difference (less than 1%) between the two lights when large fields are used.

To evaluate this hypothesis, we examined the dichromatic coefficients on those observers who were able to return for further testing.

EXPERIMENT 2: DICHROMATIC COEFFICIENTS AS A FUNCTION OF FIELD SIZE

The purpose of the second experiment was to determine whether the dichromats would accept a dichromatic match using 450 and 650 nm primaries as the field size was increased to 8°. Since the procedure took 3–4 h, only a few of the original 18 observers were able to participate.

 Procedure. We used primaries of 450 nm (blue) and 650 nm (red) in the mixture field and a series of four wavelengths, 589, 545, 523, and 494 nm in the test field. The field luminance varied between 5 and 15 candles/m², depending upon wavelength and class of observer. Six of the deuteranopes and four of the protanopes were studied. For each test wavelength and field size, the observer was asked to find an exact color match by adjusting the ratio of blue to red in the mixture field and the luminance of the test field. In addition, protanopes SY and CB and deuteranopes DK and MM were asked to match 494 nm using the 8° annular field stop.

Results and discussion. All six dichromats could match 589, 545, 523, and 494 nm to mixtures of 450 and 650 nm when 1° and 2° fields were used (Table II). Some accepted the matches with a 4° field. None would make such matches with the 8° field.

Three protanopes could match 589, 545, and 523 nm to mixtures of 450 and 650 nm when 1° and 2° fields were used (Table II). Two protanopes rejected the 494 nm match with the 2° field, although both had accepted the match on their first visit to the laboratory. One other, SY, was somewhat fussy about the matches even with a 1° field. This protanope also had made a full set of dichromatic matches with the 2° field on an early visit. The field-size data of Table II, collected six months later, reflect many hours of practice. Protanope DP accepted matches to test wavelengths 545 and 523 nm with the 4° field and could match the 523 nm test with
TABLE II. Dichromatic matches accepted or rejected by deuteranopes and protanopes as a function of field size.

<table>
<thead>
<tr>
<th>Field size</th>
<th>1°</th>
<th>2°</th>
<th>4°</th>
<th>8°</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 2, 3, 4a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1, 2, 3, 4b</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1, 2, 3, 4c</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1, 2, 3, 4d</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Deuteranopes

DK   √   √   x   x
MM   √   √   x   x
KK   √   √   x   x
JK   √   √   x   x
DR   √   √   x   x
MB   √   xx   √   x

Protanopes

DP   √   √   √   x   x   √   x   xx   √   x
SY   √   ?   ?   √   x   x   √   x   √   x   √   x   x
CB   √   √   √   x   x   √   x   x   x   x   x
DS   √   √   x   x   x   x

√   Match
x   No match
?   Unstable match

*Single entry means all four test wavelengths were accepted or rejected. Multiple checks are referred to numeral above.

the 8° field.

The four dichromats tested with the 8° annular field refused the 494 nm match. Thus our results cannot be attributed to the Maxwell spot or to other retinal inhomogeneity that normal trichromats observe in certain large-field conditions. The Maxwell spot subdents an ill-defined ellipse with major axis horizontal, extending 1° or 2°. The spot follows fixation and is best observed by switching rapidly from one colorimetric field to another. For normal trichromats, the phenomenon does not interfere with setting a large-field color match. With the 8° field, two dichromats spontaneously reported observing an area of color difference, a "red" spot that moved with fixation. They were instructed, as we instruct normal trichromats, to ignore the spot and were able to do so.

Many of the dichromats in Jaeger and Kroker's study accepted a neutral point match using a 22° field. We do not confirm this finding and presume the discrepancy reflects procedural differences: we used spectral primaries, while Jaeger and Kroker used colored papers on a rotating color wheel. We do agree with Jaeger and Kroker in finding, for the intermediate field sizes, that more protanopes than deuteranopes will reject a neutral point match.

The failure to obtain a large-field match of 589 to 450 and 650 nm shows that the dichromats were not relying on saturation differences to discriminate 589 and 650 nm. If dichromats refuse large-field dichromatic matches, some visual photopigment must be exerting an independent effect. To determine whether this photopigment is a normal or an anomalous cone photopigment, we examined a series of red-green color matches.

EXPERIMENT 3: RED-GREEN COLOR MATCHES FOR VARIOUS TEST WAVELENGTHS

Rods are known to be active in large-field matches of normal trichromats. Experiment 3 was designed to ask whether large-field dichromatic matches agreed with matches of normal trichromats or anomalous trichromats, or whether they showed evidence of rod mediation. The results may clarify instances where dichromats have shown some trichromatic activity with large test fields.

Procedure. We used primaries of 545 nm (green) and 670 nm (red) in the mixture field and a series of six wavelengths, 610, 596, 589, 580, 570, and 555 nm in the test field. The field luminance was about 5 candles/m². The six deuteranopes and four protanopes of experiment 2 were observers. First, using the 2° field for each test wavelength, the observers were asked to adjust the test luminance to give the best color match for nine red/green ratios covering the full range of the red-green dial. Then, using the 8° field for each test wavelength, a match range was established with the experimenter setting the red/green mixture. The match range is the set of primary mixtures for which the observer can obtain a color match by adjustment of the test wavelength luminance.

Results and discussion. The results for the 8° field are shown in Table III as the proportion of 670 nm light in the mixture at the extremes of the match range, together with the proportion of 670 nm light for the match for a normal trichromat, a protanomalous, and a deuteranomalous match. Except for the 555 nm test wavelength and a few matches for two deuteranopes, the deuteranopes' matches require more red primary than the deuteranomalous match. The matches for protanopes occur near the protanomalous match, but consistently contain a greater fraction of R primary than protanomalous matches. Previous reports of failure of large-field dichromatic matches did not include a study of metamers. The discrepancy between our data and those of Nagel may have been attributed to one of two possibilities: Nagel might be attributed to one of two possibilities: Nagel may have been an extreme anomalous trichromat; alternatively, if indeed a dichromat, he would not be accurate in color naming. We have noted that color names of dichromats with large fields are dependent on intensity and contrast in the field. The dichromats show heightened color contrast similar to that found in small fields or when anomalous trichromats make color judgments.

Our data suggest that the ability to make unique red-green matches is a general feature of protanopia and deuteranopia which occurs reliably with fields of 8° or more. Ruddock showed that dichromats could make dichromatic matches with two 1° 45' fields, one the mixture field, fixated foveally and the other the spectral field at 6° parafoveal. The protanopes differed in their parafoveal matches. Ruddock speculated that differing rod inputs to luminance and/or chromatic channels
mixture. These matches are shown for the 2° field primary plus the proportion of green primary in the visual photopigment response to the proportion of red primary match to a given mixture represents the total luminance. When the test-wavelength luminance is behaved as monochromats, a red-green ratio which satisfies the quantal match. For each test wavelength, there is a unique matching length sensitive visual photopigments (MWS and LWS). In normal trichromats, red-green matches with a 10 or 20 field are mediated by the middle- and long-wave-sensitive visual photopigment (SWS) does not participate in the matches. The fact that these observers exhibit narrow matching ranges in agreement with the other deuteranopes at above 540 nm, the short-wavelength-sensitive visual photopigment does not give reliable trichromatic behavior.

**Analysis of red-green matches.** For small fields, the two halves of the colorimetric field appear identical when the quantal catches for each half of the field are equal for each active visual photopigment. A match which satisfies this condition is called a quantal match.

In the anomaloscope, with both primaries chosen above 540 nm, the short-wavelength-sensitive visual photopigment (SWS) does not participate in the matches. In normal trichromats, red-green matches with a 1° or a 2° field are mediated by the middle- and long-wavelength sensitive visual photopigments (MWS and LWS). For each test wavelength, there is a unique matching red-green ratio which satisfies the quantal match.

With a 1° or a 2° field, protanopes and deuteranopes behave as monochromats, matching each red-green mixture with a suitable amount of test-wavelength luminance. When the test-wavelength luminance is plotted as a function of red-green mixture, the luminance match to a given mixture represents the total visual photopigment response to the proportion of red primary plus the proportion of green primary in the mixture. These matches are shown for the 2° field (Figs. 1–6) for the six deuteranopes (right panel) and four protanopes (left panel) for test wavelengths 555 to 610 nm. The vertical bars show the interobserver match range. Near the primaries, some of the observers did not report a full color match, but only a brightness match.

We consider dichromacy as a reduction system of normal trichromacy, assuming that protanopes have the normal MWS and deuteranopes the normal LWS visual photopigment. When protanopic and deuteranopic luminance matches are superimposed, the intersection represents the unique red-green mixture where both the MWS and LWS photopigments have an equivalent quantal catch for the test and the mixture fields. The 2° match for a group of normal trichromats should occur at the intersection of protanopic and deuteranopic

**FIG. 1.** Anomaloscope matches made by protanopes [panel (a)] and deuteranopes [panel (b)] to a 555 nm test field. The solid line with vertical bars shows color and luminance matches made by four protanopes and six deuteranopes using the 2° field. The dashed line shows predicted scotopic luminance matches. The solid bar is the unique matching range for protanope CB [panel (a)] and deuteranope DR [panel (b)] using the 8° field. The arrows under the letters N, PA, and DA point to the matches made by a normal, a protanomalous, and a deuteranomalous trichromat, respectively.

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**TABLE III.** Proportion of red in red (670 nm)–green (545 nm) mixtures matched to various test wavelengths.

<table>
<thead>
<tr>
<th>Test Wavelength</th>
<th>610</th>
<th>596</th>
<th>589</th>
<th>580</th>
<th>570</th>
<th>555</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Deuteranopes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DR</td>
<td>0.957</td>
<td>0.907</td>
<td>0.837</td>
<td>0.735</td>
<td>0.527</td>
<td>0.0</td>
</tr>
<tr>
<td>KK</td>
<td>0.950</td>
<td>0.850</td>
<td>0.722</td>
<td>0.700</td>
<td>0.350</td>
<td>0.0</td>
</tr>
<tr>
<td>JK</td>
<td>0.950</td>
<td>0.850</td>
<td>0.677</td>
<td>0.515</td>
<td>0.308</td>
<td>0.0</td>
</tr>
<tr>
<td>MM</td>
<td>0.967</td>
<td>0.867</td>
<td>0.747</td>
<td>0.515</td>
<td>0.308</td>
<td>0.0</td>
</tr>
<tr>
<td>DK</td>
<td>0.960</td>
<td>0.860</td>
<td>0.867</td>
<td>0.400</td>
<td>0.180</td>
<td>0.0</td>
</tr>
<tr>
<td>MB</td>
<td>0.960</td>
<td>0.860</td>
<td>0.867</td>
<td>0.307</td>
<td>0.140</td>
<td>0.0</td>
</tr>
<tr>
<td>Prediction</td>
<td>0.966</td>
<td>0.919</td>
<td>0.869</td>
<td>0.788</td>
<td>0.650</td>
<td>0.195</td>
</tr>
<tr>
<td><strong>Protanopes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CB</td>
<td>0.985</td>
<td>0.965</td>
<td>0.930</td>
<td>0.925</td>
<td>0.867</td>
<td>0.0</td>
</tr>
<tr>
<td>SY</td>
<td>0.985</td>
<td>0.972</td>
<td>0.937</td>
<td>0.920</td>
<td>0.867</td>
<td>0.0</td>
</tr>
<tr>
<td>DP</td>
<td>0.990</td>
<td>0.972</td>
<td>0.930</td>
<td>0.720</td>
<td>0.100</td>
<td>0.0</td>
</tr>
<tr>
<td>DS</td>
<td>0.972</td>
<td>0.972</td>
<td>0.937</td>
<td>0.972</td>
<td>0.880</td>
<td>0.0</td>
</tr>
<tr>
<td>Prediction</td>
<td>0.994</td>
<td>0.981</td>
<td>0.960</td>
<td>0.936</td>
<td>0.912</td>
<td>0.0</td>
</tr>
<tr>
<td>Normal</td>
<td>0.795</td>
<td>0.655</td>
<td>0.543</td>
<td>0.400</td>
<td>0.283</td>
<td>0.0</td>
</tr>
<tr>
<td>PA</td>
<td>0.950</td>
<td>0.917</td>
<td>0.907</td>
<td>0.837</td>
<td>0.732</td>
<td>0.0</td>
</tr>
<tr>
<td>DA</td>
<td>0.400</td>
<td>0.255</td>
<td>0.180</td>
<td>0.140</td>
<td>0.085</td>
<td>0.0</td>
</tr>
</tbody>
</table>

luminance matches provided all three groups of observers are similar in their inert pigment characteristics. Given the small number of observers, this expectation is well realized. Protanomalous and deuteranomalous trichromats do not accept the normal match: their visual photopigments differ from those of normals. Their unique matches represent intersection points of their underlying photopigments.

Mid-match points. The plots in Figs. 1–6 present a graphical representation rather than the usual sets of linear equations. The unique matches made by a deuteranope, DR, and a protanope, CB, with the 8° field are shown as solid bars. The luminance settings indicate that the 8° matches were also matches for the 2° field. For wavelengths 570–610, matches for deuteranope DR contain a higher proportion of red primary than those of normal or deuteranomalous trichromats; matches for protanope CB contain a higher proportion of red than those of normal or protanomalous trichromats.

These matches are mediated by at least one visual photopigment which does not act in the 2° matches of normals, anomalous trichromats, or dichromats.

To evaluate the possibility that the matches were rod-mediated, we calculated the luminance matches that would be made if rods alone mediated the response. These theoretical matches based upon the CIE scotopic luminosity function, $V_x$, are shown in Figs. 1–6 as a dashed line. Matches for the deuteranope DR and the protanope CB occur at or near the intersections of the theoretical rod luminance matches with the 2° luminance matches of the dichromats. The intersection points are included in Table III to allow comparison of the predictions with match positions of the other observers. The large-field matches of our dichromats are quantal matches, mediated by the photoreceptors of small-field dichromacy plus a photoreceptor with the spectral sensitivity of rhodopsin.

Match width. The match widths are strongly correlated with the difference in slope between the rod luminance function and the dichromatic luminance function. The match widths are narrowest at 610 nm where the rod function is steepest, and broadest at 555 nm where rod function is shallowest. In general, the protanopic match widths are narrower than deuteranopic match widths. This trend reverses at 555 nm where the rod and 2' protanopic luminance matches almost coincide over their range. The characteristic match width profile strengthens our evidence that the matches are mediated by the dichromatic cone photopigment and a visual photopigment whose spectral sensitivity is that of rhodopsin.

EXPERIMENT 4: MATCHES AS A FUNCTION OF INTENSITY

When rods participate in large-field matches made by normal trichromats, quantal matches are rarely made.
Clarke uses the term tetrachromacy to allow for the activity of rods in normal color matching. There are three important properties of normal trichromacy which are not fulfilled in tetrachromacy. Normal trichromacy has the properties that (a) three primaries are sufficient for spectral color matching; (b) the relationship between the primaries is invariant, that is, the matches are unique; (c) they hold over a range of 1500 td. These are all properties of quantal matches. With an 8° field, three primaries are sufficient and a unique match is made. However, the matches change with field luminance. If four primaries are allowed, the matches are not unique. Trezona devised a four-primary method of systematically iterating between matches made at a scotopic and mesopic luminance until a unique match was achieved. This unique match is a quantal match for each of the four visual photopigments, and is therefore intensity invariant. Experiment 4 was designed to test whether the dichromatic matches would hold with reduction in field luminance.

**Procedure.** We used primaries of 545 nm (green) and 670 nm (red) in the mixture field and a series of three wavelengths, 610, 589, and 570 nm in the test field. The highest field luminance was about 5 candles/m². The luminance was reduced in one-log-unit steps for a range of 3 log units. Light shielding was provided for the lowest intensities. The observers adapted to the field for up to 30 min. in the low ambient illumination of the darkened room. Two deuteranopes and two protanopes were observers. For each test wavelength and test luminance, a match range was established by the experimenter using the 8° field.

**Results and discussion.** The matches are plotted for each luminance and test wavelength in Fig. 7. The sets of matches show similar trends. Matches are not affected by a tenfold reduction of intensity. The matches tend to widen somewhat with a one-hundred-fold reduction and show greater widening with the one-thousand-fold reduction of luminance. There is no shift of the match midpoint to a higher or lower fraction R. The 5 cd/m² match is always accepted. These data show an intensity invariance of the quantal matches with a 1000 to 1 change in luminance.

**THEORETICAL IMPLICATIONS**

**Implications for normal trichromacy.** The protanopic and deuteranopic 8° matches may be compared with the 2° and the 8° matches made by normal trichromats (Table IV). The large-field trichromacy we observe in protanopes and deuteranopes shows the properties of a unique match and intensity invariance. The matches therefore show properties more similar to those of normal small-field trichromacy than of normal large-field

**TABLE IV.** Comparison of trichromacy and tetrachromacy in normal trichromats with large-field trichromacy in protanopes and deuteranopes.

<table>
<thead>
<tr>
<th>Query</th>
<th>Small-field</th>
<th>Large-field</th>
<th>Large-field trichromacy in protanopes and deuteranopes</th>
</tr>
</thead>
<tbody>
<tr>
<td>How many primaries?</td>
<td>3</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Are unique matches made?</td>
<td>Yes</td>
<td>Yes</td>
<td>No*</td>
</tr>
<tr>
<td>Are matches intensity-invariant?</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
</tbody>
</table>

*An exception is the technique proposed by Trezona.*
tetachromacy.

The comparison points to a distinction between large-field matches of normals and dichromats. Normal trichromacy is both pigment and channel limited. With small fields, normal trichromacy is pigment limited: there are three cone visual photopigments, and at least three processing channels.\(^{41}\) Intensity-invariant quantal matches are made. With large fields, normal trichromacy is not pigment limited; there are four (three cones and one rod) visual photopigments. However, trichromatic matches can be made: they are not intensity invariant, nor are they quantal. These data indicate that the rods do not have an independent channel; their signals are carried on the channels carrying cone achromatic and chromatic information. In this sense, we say that the data are channel limited. There are only three orthogonal channels for color mixture.

Psychophysical study of rod-cone interactions show a variety of effects, reviewed by Jacobs,\(^{42}\) including mutual facilitation and mutual inhibition. McCann and Benton\(^{2}\) report that rods interacting with LWS cones yield an array of colors similar in color appearance to photopic mixtures of wavelengths 495 and 656 nm. Stabell and Stabell\(^{5}\) note that rod color does not occupy a unique locus in the CIE diagram. Jacobs\(^{42}\) observes that the rod interactions reported by Stabell and Stabell suggest that rods interact in the opponent chromatic channels. Thus, although rods do not have an independent activity in color matching, they can modulate opponent color signals.

A neurophysiological basis may be noted in data from macaque monkeys.\(^{25}\) When rods enter the chromatic opponent, the rod response is that of the field center. The four receptive field types (red on-center, red off-center, green on-center, green off-center) would yield two distinctly different types of opponent response. Thus a red-\(V'_r\) on-center or a red-\(V'_g\) off-center would give different responses from a green-\(V'_r\) on-center or a green-\(V'_g\) off-center. In psychophysics, the four types of receptive field are treated as one chromatic opponent. Both the psychophysics\(^{23,24}\) and the Wiesel and Hubel\(^{25}\) data make it clear that any explanation of rod effects on color appearance requires a more complex approach than is presently available in color theory.

**Theoretical interpretation of large-field dichromatic data.** The intensity-invariant quantal matches made by our dichromats suggest to us that three cone-rod channels are available to protanopes and deuteranopes. Small-field dichromatic matches are pigment limited; there are two cone visual photopigments and at least two processing channels. With large fields, there are three (two cones and one rod) visual photopigments and we suggest that there are at least three channels. The third channel may reflect rod activity in a residual red-green opponent system. Alternatively, two neural channels may be formed from a blue-yellow channel in a manner similar to that discussed for the red-green channel of normal trichromats. The important point is that the rod signal has independent recognition in dichromatic color opponent channels, allowing the large-field trichromacy.

An alternative explanation of our data is that the dichromats have only two processing channels, but reject all but the quantal match because of differing temporal and spatial transients\(^{27}\) generated by cones and rods along the border of the test and matching fields. An unsatisfactory aspect of this explanation is that it implies that only dichromats, and not normal trichromats, are able to use such transient information to make large-field quantal matches under the free-view conditions that we use. We would expect that the use of the 8° annular stop with steady fixation on the black center would reduce information due to temporal border transients. Our observers refused classical dichromatic matches when the annular field was used (experiments 1 and 2).\(^{27}\) We suspect that while border transients may enhance color information for dichromats, they are not the cause of the large-field color-matching behavior.

A third possibility is that the trichromacy is not mediated by normal rods. Possibly, the dichromats have cones whose photopigment has the spectral response of rhodopsin as postulated for some of the monochromacies.\(^{30-32}\) If the latter is true, then protanopia and deuteranopia should be regarded as additional forms of anomalous trichromacy. If mediated by normal rods, the term dichromacy may be regarded as a special case of reduced color vision elicited when the small fields selectively allow cone response.

**Do dichromats have a unique sensory percept for red?** The impetus for our study was the fact that many dichromats insist that they have a unique sensory percept for "red." Our study is one of color matches which does not tell us anything about the color perceptions of dichromats. However, the fact that protanopes and deuteranopes become trichromatic with large fields means that they do have both the photopigment and possibly the processing channel that would permit an added unique sensory percept. We suspect that their color world is weak compared with that of normal trichromats. However, they do have trichromatic color vision for large fields and it may well be that this trichromacy forms the basis for the perceptual claims made by dichromats.

**ACKNOWLEDGMENTS**

The major impetus for this research came from a deuteranope, Michael Breton, who insists that he enjoys a unique sensory percept for red. We thank our research subjects for their cooperation.

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6See R. M. Boynton and H. Scheibner, "On the perception of red by 'red blind' observers," Acta Chromatica 1, 205–220 (1967). We used such explanations with dichromatic observers.


26The suggestion that spatial and temporal border transients could explain our data was first made by D. I. A. MacLeod at the annual meeting of A.R.V.O. in 1976.

27We attempted to evaluate the effects of border transients in two additional ways. We constructed an 8° field stop with a 2° black bar. The 2° bar prevents an observer from making direct comparisons across the test-field border. With this test field, discrimination deteriorated. However, protanopes SY and CB and deuteranopes DK and MM continued to reject the neutral point match of 494 nm to a mixture of 450 and 650 nm. Their red-green matches for wavelengths 570, 589, and 610 nm widened, similar to those for one-thousand-fold reduction in field luminance (Fig. 7). Our second approach was to defocus the field so that the border was invisible. Again, discrimination was reduced, but not to the same degree as with the 2° bar separating the test and mixture fields.


