Vision Research 48 (2008) 2599–2603

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

# Protanomaly without darkened red is deuteranopia with rods

Steven K. Shevell [a,b,*], Yang Sun [a], Maureen Neitz [c]

[a] Department of Psychology, University of Chicago, USA
[b] Department of Ophthalmology and Visual Science, University of Chicago, USA
[c] Department of Ophthalmology, Medical College of Wisconsin, USA

ARTICLE INFO

*Article history:*
Received 30 October 2007
Received in revised form 21 February 2008

*Keywords:*
Color vision defect
Rayleigh match
Dichromacy

ABSTRACT

The Rayleigh match, a color match between a mixture of 545 + 670 nm lights and 589 nm light in modern instruments, is the definitive measurement for the diagnosis of inherited red–green color defects. All trichromats, whether normal or anomalous, have a limited range of 545 + 670 nm mixtures they perceive to match 589 nm: a typical color-normal match range is about 50–55% of 670 nm in the mixture (deutan mode), while deuteranomals have a range that includes mixtures with less 670 nm than normal and protanomals a range that includes mixtures with more 670 nm than normal. Further, the matching luminance of the 589 nm light for deuteranomals is the same as for normals but for protanomals is below normal. An example of an unexpected Rayleigh match, therefore, is a match range above normal (typical of protanomaly) and a normal luminance setting for 589 nm (typical of deuteranomaly), a match called protanomaly "when the red end of the spectrum is not darkened" [Pickford, R.W. (1950). Three pedigrees for color blindness. *Nature*, 165, 182.]. In this case, Rayleigh matching does not yield a clear diagnosis. Aside from Pickford, we are aware of only one other report of a similar observer [Pokorny, J., & Smith, V. C. (1981). A variant of red–green color defect. *Vision Research*, 21, 311–317]; this study predated modern genetic techniques that can reveal the cone photopigment(s) in the red–green range. We recently had the opportunity to conduct genetic and psychophysical tests on such an observer. Genetic results predict he is a deuteranope. His Rayleigh match is consistent with L cones and a contribution from rods. Further, with a rod-suppressing background, his Rayleigh match is characteristic of a single L-cone photopigment (deuteranopia).



## 1. Introduction

About 8% of men have inherited red–green color deficiency, making it the most common type of color vision abnormality. Far fewer women are affected (about 0.5%) because the cause is an abnormal photopigment gene on the X-chromosome (Nathans, Thomas, & Hogness, 1986). Men have one X-chromosome but women have two; if either one of a woman's X-chromosomes has normal cone-pigment genes then her color vision is essentially normal (though see Schmidt, 1934).

Red–green color deficiency is classified into four recognized sub-types. For all sub-types, an abnormal gene results in either no functional M cones or no functional L cones. For two of the sub-types there is only one active photopigment in the red–green range: either an L pigment or an M pigment. Individuals with these sub-types are called, respectively, deuteranopes or protanopes, and have dichromatic color vision. For the other two sub-types, color vision is trichromatic, as for color normals, but the two photopigments in the red–green range are not the same as normal ones. In deuteranomalous trichromacy there are two distinct photopigments, both of which are similar to the normal L pigment (there is no cone with an M pigment). In protanomalous trichromacy, the two distinct photopigments are similar to the normal M pigment (no cone has an L pigment). Further sub-divisions split each type of anomalous trichromacy into 'simple' and 'extreme' subgroups according to the preserved degree of chromatic discrimination (Franceschetti, 1928; Pokorny & Smith, 1982).

These sub-types of red–green color defect are defined according to an individual's color matches. Definitive diagnosis is made with the Rayleigh match (Rayleigh, 1881), which in modern instruments is a match of a 589 nm light to an admixture of 545 + 670 nm. In a typical instrument, one knob varies the proportion of 670 nm light in the admixture from 0% (pure 545 nm) through 50% (half 545 nm, half 670 nm) to 100% (pure 670 nm). By convention the maximum levels of 545 nm and 670 nm are fixed so that 100% of either wavelength equally stimulates L cones (so-called 'deutan mode'; Mitchell & Rushton, 1971; Pokorny, Smith, & Katz, 1973). The second knob varies the radiance of the 589 nm field. All observers––normals, anomalous trichromats and dichromats––can make a match by adjusting the two knobs.

* Corresponding author. Address: Visual Science Laboratories, University of Chicago, 940 East 57th Street, Chicago, IL 60637, USA. Fax: +1 773 702 0939.
*E-mail address:* shevell@uchicago.edu (S.K. Shevell).

0042-6989/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2008.03.001

Distinctive features of the Rayleigh match characterize each sub-type of red–green color deficiency as well as normal color vision. Consider first color normals, who perceive a color match only when the admixture has about 50% of 670 nm light. At a lower (higher) percentage the mixture field appears more greenish (reddish) than 589 nm. The Rayleigh match also reveals the radiance of 589 nm light required for the match. Theoretically, the number of quanta absorbed by each type of cone, M and L, is identical for the 545 + 670 nm admixture and for the 589 nm light so only a unique mixture proportion and unique radiance of 589 nm should give a match. Chromatic discrimination, however, is not exact so Rayleigh-match measurements actually yield a narrow range of mixture ratios that are not discriminated from 589 nm. For color normals this range is 5% or less (about 50–55% of 670 nm in the admixture is perceived to match 589 nm).

Dichromats, who have only one photopigment in the red–green range, can match 589 nm to every admixture proportion (that is, any proportion in the range from 0% to 100%). Each proportion establishes some level of quantal absorption for the single cone pigment in the red–green range, and this level can be equaled by setting an appropriate radiance of the 589 nm field. The relation between the 589 nm setting and the mixture proportion distinguishes deuteranopes from protanopes. Recall that the maximum levels of 545 and 670 nm are set to stimulate L cones equally (deutan mode). For deuteranopes, therefore, any mixture proportion has the same L-cone stimulation, which of course is matched by a constant radiance of 589 nm. Thus, the matching 589 nm radiance does not vary with the proportion of 670 nm in the admixture. Protanopes, on the other hand, have only an M cone, which is far more sensitive to 545 than 670 nm. As the amount of 670 nm in the mixture increases (and, correspondingly, 545 nm decreases), the protanope's M cone is less stimulated so the percept of the mixture becomes less bright, requiring a lower radiance of 589 nm for the match. For protanopes, therefore, the 589 nm radiance decreases as the proportion of 670 nm in the admixture increases. This reduction in brightness with increasing 670 nm in the mixture has been termed "darkened" red though note that a dichromat cannot perceive a shift in hue toward redness with increasing 670 nm in the admixture (a color normal—perhaps the color-test examiner—sees the redness).

Deuteranomalous trichromats have two pigments in the red–green range so do not accept a match between 589 nm and every mixture proportion. Their degree of chromatic discrimination, which is quantified by the range of 670 nm proportions not discriminated from 589 nm, depends on the similarity of the two pigments, both of which are close to the normal L. If the two pigments have very similar spectral sensitivities (1 nm difference in the wavelengths of peak sensitivity and the same optical density), the two cones' responses are very highly correlated so chromatic discrimination is poor and the match range is wide. If, however, the two pigments are separated by as little as 2 nm, then the cones' responses are sufficiently different to give substantially better chromatic discrimination and thus a narrower match range (He & Shevell, 1995). The center of this range for deuteranomals is typically 25–30% of 670 nm light in the admixture, which is less 670 nm light than normal. The variation in match range among deuteranomalous trichromats is huge because match range is highly sensitive to the similarity of the two pigments. Some deuteranomals have a range comparable to normal (5%, e.g., 20–25% admixture range) while others have a range over 50% (0–55% admixture range). Both pigments of a deuteranomalous trichromat are similar to the normal L, so any admixture proportion accepted as a match to 589 nm will require virtually the same radiance of 589 nm because of the deutan-mode property of the measuring instrument.

The match range of protanomalous trichromats follows similar reasoning to that for deuteranomalous trichromats. The range often will be wider than the normal's because a protanomal's cone pigments, both of which are similar to the normal M, can have spectral sensitivities too similar to each other to support good chromatic discrimination. The center of a protanomalous match range is at a higher proportion of 670 nm in the admixture than for the normal, and large individual differences in match range reflect the degree of difference in an individual's two cones' spectral sensitivities. Both cones are similar to the normal M so are less stimulated as the proportion of 670 nm in the mixture increases. Thus protanomals, with their higher proportion of 670 nm in the admixture than color normals, set a lower radiance of matching 589 nm light (that is, darkened red) compared to normals or deuteranomals.

The properties of Rayleigh matches described above can be gleaned by plotting for a given cone photopigment the relative radiance of 589 nm light that gives the same cone stimulation as a 545 + 670 nm admixture, as a function of the proportion of 670 nm light in the mixture (Fig. 1; after Thomas & Mollon, 2004). Each line represents a different photopigment. For example, the two solid lines are for cones with spectral sensitivity peaks near the typical L cone (553 and 558 nm), and therefore are representative of deuteranomaly (no M cones). The two lines cross near 25% of 670 nm in the admixture, which is the exact quantal match for the two particular pigments shown. An individual deuteranomal's match range depends on the similarity of the two cones' spectral sensitivities, which plots as the similarity of the two lines' slopes (more similar slopes imply a larger match range). The ellipse near the lines' intersection suggests schematically the match width for an observer with two pigments 5 nm apart. Both lines are nearly horizontal owing to the deutan-mode convention for Rayleigh matching.

Protanomalous trichromats have two cones with spectral sensitivities near the normal M (535 and 540 nm in Fig. 1, dashed lines). The lines representing these cones intersect near 87% of 670 nm in the admixture. Both lines' negative slopes are characteristic of 'darkened red' in that these photopigments are much less sensitive to 670 than 545 nm light.

This lengthy introduction to the Rayleigh-match admixture range and 589 nm matching radiance reveals that a particular Rayleigh-match measurement is never expected: a protanomalous admixture range (more 670 nm in the admixture than normal) but without an accompanying reduction of the 589 nm radiance as the proportion of 670 nm in the admixture increases. In this case, the Rayleigh match fails to give a clear diagnosis of the type of color vision defect. This unanticipated outcome, protanomaly without darkened red, has been reported twice to our knowledge: initially by Pickford (1950) in less than a sentence and thirty years later by Pokorny and Smith (1981), who made thorough measurements on an 18-year-old male. Both previous studies precede modern genetics, which allow determination of the cone photopigments in the red–green range that underlie an individual's Rayleigh match. We recently came across an observer with a protanomalous admixture-proportion range but without darkened red (that is, without a reduction of 589 nm matching radiance with increasing 670 nm in the mixture), and were able to conduct both psychophysical and genetic tests.

## 2. Methods

### 2.1. Psychophysical stimuli and procedures

Two standard color tests were administered: Rayleigh matching using a Neitz anomaloscope (Pokorny, 1981), and the FM-100 hue test (Farnsworth, 1957). Rayleigh matches were measured using the Linksz (1964) procedure in which the

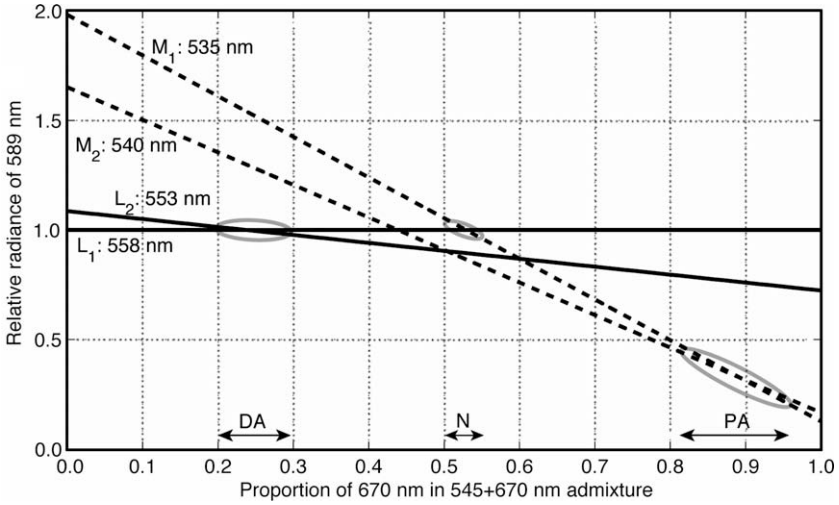


**Fig. 1.** The relative radiance of 589 nm light (vertical axis) giving the same quantal absorption as a particular proportion of 670 nm light in a 545 + 670 nm mixture (deutan mode, horizontal axis), for a given photopigment. Values are shown for four different photopigments (spectral sensitivity peak at 535, 540, 553 or 558 nm). Ellipses show typical matches of color normals (N) near the intersection of the 535 and 558 nm lines; simple deuteranomalous trichromats (DA) near the intersection of the 553 and 558 nm lines; and simple protanomalous trichromats (PA) near the intersection of the 535 and 540 nm lines. The range of matching proportions for DA, N and PA observers are projected from the ellipses and shown as arrows above the horizontal axis.

experimenter set the admixture proportion and the observer sought a match by varying only the 589 nm radiance. The observer reported that the admixture field was redder than, greener than or a match to 589 nm.

Heterochromatic flicker photometric matches (HFP) were measured between the R (Judd 1951 chromaticity $x = 0.625$, $y = 0.344$) and G ($x = 0.282$, $y = 0.613$) phosphors of a color CRT (Sony GDM-F520). The flicker rate was 12.5 Hz; the field was a square 1.6° wide. The R phosphor was fixed at 9 cd/m2; the observer adjusted the luminance of the G phosphor for minimum flicker.

A Maxwellian-view optical system (Shevell & Humanski, 1988) was used for Rayleigh matches on a 3.2° diameter chromatic background chosen to suppress rods (500 nm at 40 photopic td = approx 300 scotopic td). A constant-luminance 60 td admixture of 540 plus 660 nm light was matched to 589 nm (2.0° diameter field). As before, testing followed the Linksz procedure.

### 2.2. DNA isolation and genetic analyses

DNA was isolated from whole blood using the Puregene DNA purification kit (Gentra Systems, Minneapolis, MN). The first gene in the X-chromosome opsin gene array was amplified and exons 2, 3, 4 and 5 of the first gene were directly sequenced (as described by Neitz et al., 2004). Two real-time quantitative polymerase chain reaction (PCR) assays were performed as described previously to determine the relative number of opsin genes and the ratio of L to M genes on the X-chromosome (Neitz & Neitz, 2001).

### 2.3. Observer

The observer was a 22-year-old male. He was an art student who was aware of some kind of color loss. Initial testing revealed a shifted Rayleigh-match admixture proportion typical of protanomaly but with color-normal radiance settings for 589 nm. After initial screening, he agreed to return to the laboratory for a full day of further testing.

## 3. Results

### 3.1. Psychophysics

#### 3.1.1. Standard Rayleigh match

The Rayleigh-match range for the right eye was 53–81% of 670 nm light in the admixture (thick gray line, Fig. 2); this rather wide range is not uncommon for protanomalous trichromats with poor chromatic discrimination (Pickford, 1958). So-called 'extreme' protanomals have a match range that extends down to the normal match at the low end. As the mixture proportion increased from 53% to 81%, the radiance of the matching 589 nm light decreased only slightly from the color-normal radiance (normalized here to 1.0) to 0.87 on this normalized scale. This is a very small reduction in the radiance of 589 nm––equivalent to 2 instrument units of Y on the Nagel anomaloscope's scale from 0 to 80 (Pokorny, Smith, Verriest, & Pinckers, 1979), and thus the matches were "without darkened red". By comparison, a typical protanomalous trichromat with a 53–81% match range would have a reduction in 589 nm radiance from 1.0 (color-normal radiance) to less than 0.5 (bottom right, Fig. 1). The range of 589 nm radiance values can be expressed as the relative-radiance ratio over the full range of matching admixtures. This radiance ratio for the observer's right eye was 1.15:1, compared to a ratio for a typical protanomal over the same admixture range of more than 2:1.

The Rayleigh match in the left eye had a much larger matching range: the 670 nm proportion in the admixture ranged from 8% to 84% (nearly dichromatic) with little change in the matching radiance of 589 nm with the increase in the 670 nm proportion (589 nm radiance ratio 1.23:1). For comparison, a typical protanomalous trichromat with this same matching-admixture range would have a radiance ratio of over 3:1 (Fig. 1).

#### 3.1.2. FM-100 hue test

Errors on the FM-100 hue test had an indeterminate red–green axis that was neither clearly protan nor deutan (Fig. 3). Error scores were 165 in the right eye and 203 in the left eye. These error scores are typical of observers with a congenital red–green color defect (Kinnear, 1970). The color-normal 95th percentile FM-100 error score is 74 (Verriest, 1963). The error score in the right eye was similar to that found for Pokorny and Smith's (1981) observer (147 in one eye, 169 in the other eye).

#### 3.1.3. HFP

Flicker photometry between the R and G phosphors of a CRT was measured separately for the right and left eye. Results for each eye were typical of a deutan color defect: the relative luminance of the R-to-G phosphors was 0.63 in the right eye and 0.59 in the left eye. This is similar to measurements in our apparatus for two deuteranopes (0.55, 0.57) and unlike the values for three color normals (0.96, 0.96, 0.97).

#### 3.1.4. A contribution from rods to the Rayleigh match?

No combination of cone pigments predicts more 670 nm than normal in the admixture together with a virtually normal radiance of 589 nm (Fig. 1), as found for this observer's right eye (Fig. 2). This result, however, is qualitatively consistent with a match

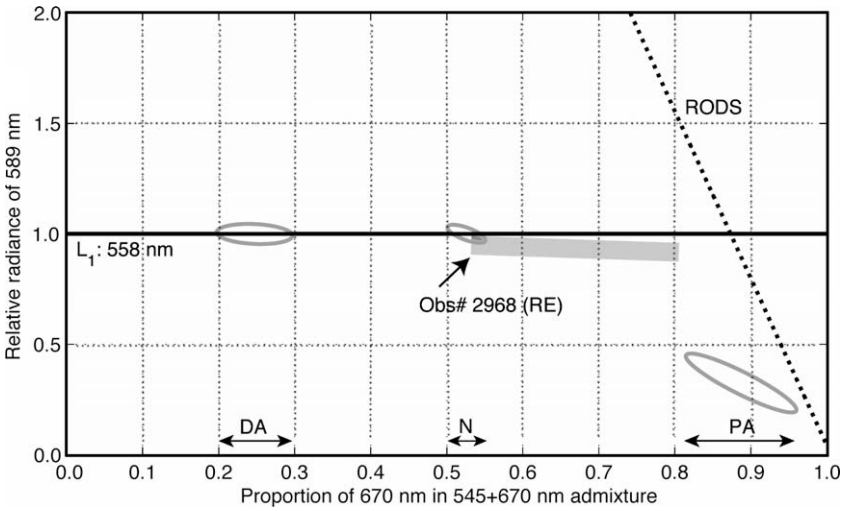


**Fig. 2.** As Fig. 1 but for only two photopigments: a cone pigment with 558 nm spectral peak and rhodopsin (RODS). The thick gray line shows the Rayleigh color-match range for the right eye of Obs.# 2968, whose settings can be characterized as protanomalous without darkened red (see text). Ellipses and arrows replotted from Fig. 1.

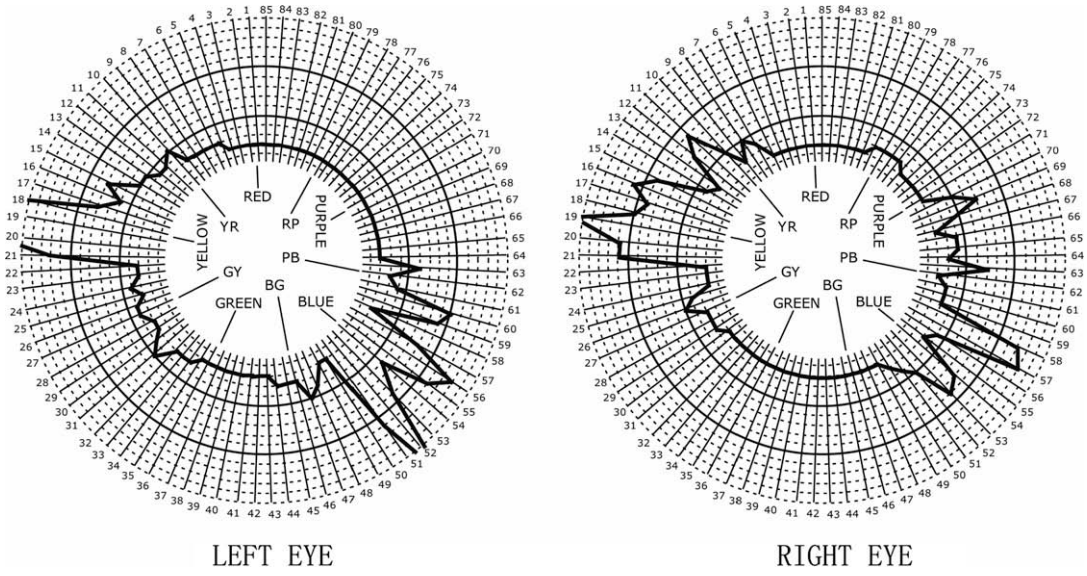


**Fig. 3.** Results from the FM-100 hue test for the left eye and right eye of Obs.# 2968.

determined by a deuteranope's L cone and rods (intersection of solid and dotted lines, Fig. 2). The nearly deuteranopic Rayleigh match in the fellow eye, and the flicker photometric matches in both eyes, are consistent with a single L cone in the red–green range. A contribution from rods is reported for the only carefully studied observer with a Rayleigh match characterized as "protanomaly without darkened red" (Pokorny & Smith, 1981).

If rods and L cones mediate the Rayleigh match, then suppressing rods should make the observer's match dichromatic. This was tested by remeasuring the Rayleigh match on a 3.2° diameter 500 nm 40 photopic td (approx 300 scotopic td) background, which suppressed rods for the Rayleigh-match wavelengths at 60 photopic td (maximum of approx 100 scotopic td; Aguilar & Stiles, 1954). A 2.0° matching stimulus, with one hemifield an admixture of 540 + 660 nm lights and the other hemifield a uniform 589 nm light, was superimposed on this background. With the rod-suppressing background, the Rayleigh match in both eyes was deuteranopic: right-eye match range from 1.6% to 99.5% of 660 nm in the admixture and with the radiance of 589 nm over this range varying over a small ratio of 1.3:1; the left-eye admixture-proportion range was the same as for the right eye and the 589 nm radiance ratio was 1.1:1. Thus, the Rayleigh match in each eye with rods suppressed was dichromatic and deuteranopic. (The lower and upper limits 1.6% and 99.5% are not meaningfully different from 0% and 100%, respectively. Neutral density wedges in this apparatus limited the least amount of 660 nm or 540 nm light in the admixture. Also, recall that the Rayleigh match in the optical system maintained constant luminance, which is close but not identical to deutan mode. For a single L pigment with spectral peak of 558 nm, the theoretical radiance ratio for a constant-luminance 540 + 660 nm admixture is about 1.5:1 over a range of 1–99% of 660 nm in the admixture.)

### 3.2. Genetic analyses

Real time PCR provided an estimate of the ratio of L:M-cone-pigment genes on the X-chromosome, expressed as a percentage of the X-chromosome opsin genes that are L. The results indicated that 100% of the X-chromosome opsin genes were L genes. A second real-time PCR assay was performed to estimate the number

of opsin genes on the X-chromosome. The result gave the percentage of the X-chromosome opsin genes downstream of the first opsin gene in the X-chromosome array; this percentage was 0%. The interpretation of these results is that the subject has a single X-chromosome opsin gene and it encodes an L-pigment opsin.

Direct sequencing of exon 5 of the X-chromosome opsin gene confirmed that the first gene in the array encoded an L opsin (Kainz, Neitz, & Neitz, 1998). The amino acids at the spectral tuning positions encoded by exons 2, 3 and 4 were serine at position 116, serine at position 180, isoleucine at position 230, alanine at position 233, and methionine at position 236. These results predict that the observer's L photopigment has a peak sensitivity of 559 nm (Carroll, Neitz, & Neitz, 2002).

In sum, the results of genetic analyses indicate that the subject has a single X-chromosome opsin gene that encodes an L opsin with predicted peak sensitivity of 559 nm. This X-chromosome opsin gene array structure is typical of a dichromat with a deuteranopic phenotype.

## 4. Discussion

The psychophysical and genetic results indicate this observer has only a single L photopigment in the red–green range. Rayleigh matches on a background field that suppressed rods were typical of deuteranopia: dichromatic and very little change in the radiance of the 589 nm light for any proportion of 660 nm in the admixture. Flicker photometry was deutan. Genetic analysis revealed a single X-chromosome opsin gene for an L photopigment with an estimated spectral peak at 559 nm. From these results, we conclude his 'protanomaly without darkened red' for the standard Rayleigh match (no background) can be accounted for by a single L pigment and rods; that is, the observer is a deuteranope whose trichromatic Rayleigh match depends also on rhodopsin.

The only other well-studied observer who can be characterized as 'protanomalous without darkened red' had spectral luminosity and absolute foveal thresholds consistent with an L photopigment (Pokorny & Smith, 1981). Rayleigh-like matches revealed activity of rhodopsin in addition to an L pigment, as here, but the matching proportion of 670 nm in the admixture varied with luminance level, which implied that an additional photopigment (besides a single L and rhodopsin) affected their observer's color matches. Unfortunately, we did not have the opportunity to repeat Rayleigh matches at multiple luminance levels but the genetic results from our observer indicate only one L photopigment in the red–green range.

Rods are well known to constrain the color matches of classically classified deuteranopes for large test fields that extend beyond the fovea (Nagy, 1980; Smith & Pokorny, 1977). The surprising feature of our observer's standard Rayleigh match in the right eye is a contribution from rods with a small test field. An open question is how his fovea came to have receptors with rhodopsin. Changes in photoreceptor topography during fetal development are consistent with rod migration toward the center of the fovea (Diaz-Araya & Provis, 1992). If foveal sparing of rods has some random variation then some small fraction of observers would have a fair number of foveal rods. The rods may be inconsequential for trichromats (normal or anomalous), whose two photopigments in the red–green range drive two distinct neural responses that support trichromatic color vision. If dichromats have the same neural pathways but only a single photopigment in the red–green range, the second pathway may carry a (perhaps weak) response from rods. For protanopes, rods and a single M photopigment would result in a protanomalous-like Rayleigh match (near the intersection of the extension of the major access of the bottom right 'PA' ellipse and the dotted rod line in Fig. 2); the result would be misclassifying a protanope as a protanomal. Only a deuteranope with foveal rods would have a perplexing Rayleigh match: protanomaly without darkened red.

## Acknowledgments

Supported by NIH grants EY-01931 (MN), EY-04802 (SS) and EY-09303 (MN), and by grants from Research to Prevent Blindness to both the University of Chicago and the Medical College of Wisconsin.

## References

Aguilar, M., & Stiles, W. S. (1954). Saturation of the rod mechanism of the retina at high levels of illumination. *Journal of Modern Optics, 1*, 59–65.
Carroll, J., Neitz, M., & Neitz, J. (2002). Estimates of L:M cone ratio from ERG flicker photometry and genetics. *Journal of Vision, 2*, 531–542.
Diaz-Araya, C., & Provis, J. M. (1992). Evidence of photoreceptor migration during early foveal development: A quantitative analysis of human fetal retinae. *Visual Neuroscience, 8*, 505–514.
Farnsworth, D. (1957). *The Farnsworth–Munsell 100 hue test manual* (revised ed.). Baltimore: Munsell Color Company.
Franceschetti, A. (1928). Die Bedeutung der Einstellungsbreite am Anomaloskop für die Diagnose der einzelnen Typen der Farbensinnstörungen nebst Bermerkungen über ihren Vererbungsmodus. *Schweizerische Medizinische Wochenschrift, 52*, 1273–1278.
He, J. C., & Shevell, S. K. (1995). Variation in color matching and discrimination among deuteranomalous trichromats: Theoretical implications of small differences in photopigments. *Vision Research, 35*, 2579–2588.
Kainz, P. M., Neitz, J., & Neitz, M. (1998). Molecular genetic detection of female carriers of protan defects. *Vision Research, 38*, 3365–3369.
Kinnear, P. R. (1970). Proposals for scoring and assessing the 100-Hue test. *Vision Research, 10*, 423–433.
Linksz, A. (1964). *An essay on color vision and clinical color-vision tests*. New York: Grune and Stratton.
Mitchell, D. E., & Rushton, W. A. H. (1971). Visual pigments in dichromats. *Vision Research, 11*, 1033–1043.
Nagy, A. L. (1980). Large field substitution Rayleigh matches of dichromats. *Journal of the Optical Society of America, 70*, 778–784.
Nathans, J., Thomas, D., & Hogness, D. S. (1986). Molecular genetics of human color vision: the genes encoding blue, green, and red pigments. *Science, 232*, 193–202.
Neitz, M., Carroll, J., Renner, A., Knau, H., Werner, J. S., & Neitz, J. (2004). Variety of genotypes in males diagnosed as dichromatic on a conventional clinical anomaloscope. *Visual Neuroscience, 21*, 205–216.
Neitz, M., & Neitz, J. (2001). A new mass screening test for color-vision deficiencies in children. *Color Research & Application, 26*, 239–249.
Pickford, R. W. (1950). Three pedigrees for colour blindness. *Nature, 165*, 182.
Pickford, R. W. (1958). A review of some problems of colour vision and colour blindness. *Advances in Science, 15*, 104–117.
Pokorny, J. (1981). *Procedures for testing colour vision––report of working group 41*. Committee on vision, assembly of behavioral and Social Sciences, National Research Council. Washington, DC: National Academy Press.
Pokorny, J., & Smith, V. C. (1981). A variant of red–green color defect. *Vision Research, 21*, 311–317.
Pokorny, J., & Smith, V. C. (1982). New observations concerning red–green color defects. *Color Research and Application, 7*, 159–164.
Pokorny, J., Smith, V. C., & Katz, I. (1973). Derivation of the photopigment absorption spectra in anomalous trichromats. *Journal of the Optical Society of America, 63*, 232–237.
Pokorny, J., Smith, V. C., Verriest, G., & Pinckers, A. J. L. G. (Eds.). (1979). *Congenital and acquired color vision defects*. New York: Grune & Stratton.
Rayleigh, L. (1881). Experiments on colour. *Nature, 25*, 64–66.
Schmidt, I. (1934/1955). Ueber manifeste Heterozygotie bei Konduktorinnen für Farbensinnstörungen. *Klinische Monatsblatter für Augenheilkunde, 92*, 456–467. [English trans. 1955. A sign of manifest heterozygosity in carriers of color deficiency. *American Journal of Optometry, 32*, 404–408].
Shevell, S. K., & Humanski, R. A. (1988). Color perception under chromatic adaptation: red/green equilibria with adapted short-wavelength-sensitive cones. *Vision Research, 28*, 1345–1356.
Smith, V. C., & Pokorny, J. (1977). Large-field trichromacy in protanopes and deuteranopes. *Journal of the Optical Society of America, 67*, 213–220.
Thomas, P. B. M., & Mollon, J. D. (2004). Modelling the Rayleigh match. *Visual Neuroscience, 21*, 477–482.
Verriest, G. (1963). Further studies on acquired deficiency of color discrimination. *Journal of the Optical Society of America, 53*, 185–195.