A-8
(4)

Reprinted from

JOURNAL

of the

OPTICAL SOCIETY

of

AMERICA

Three pigments in normal and anomalous color vision

Donald I. A. MacLeod

Institute of Molecular Biophysics, The Florida State University, Tallahassee, Florida 32306

Mary Hayhoe

Psychological Laboratory, University of Cambridge, Cambridge CB2 3EB, England

pp. 92–96

JANUARY
1974

VOLUME 64 NUMBER 1

Reprinted from:
JOURNAL OF THE OPTICAL SOCIETY OF AMERICA VOLUME 64, NUMBER 1 JANUARY 1974

Three pigments in normal and anomalous color vision*

Donald I. A. MacLeod
Institute of Molecular Biophysics, The Florida State University, Tallahassee, Florida 32306

Mary Hayhoe
Psychological Laboratory, University of Cambridge, Cambridge CB2 3EB, England
(Received 14 June 1973)

We show that the color matches of normal and anomalous trichromatic observers, taken together, uniquely determine the spectral sensitivities of the normal red- and green-sensitive pigments for wavelengths longer than about 530 nm. The key assumptions are (i) that a visual match is a match for the pigments; and (ii) that one pigment is common to normal and deutan observers, another to normal and protan observers. Calculated spectral sensitivities for these two pigments agree closely with the luminosity curves of protanopes and deuteranopes. We show also that simple protanomalous and deuteranomalous observers may share a third (anomalous) pigment. The spectral sensitivity calculated for this pigment is reasonably consistent with recent measurements on anomalous vision.

Index Headings: Color; Vision.

When spectrally different lights are indistinguishable to normal vision, they are also indistinguishable from one another in their excitation of erythrolabe and chorolabe, the red- and green-sensitive visual pigments of the normal eye.[1] But people with anomalous color vision distinguish between spectrally different colors that look the same to normal eyes. The anomalous eye must contain another visual pigment that has a spectral sensitivity such that lights that are equal to one another in their effects upon each of the normal pigments need not have equal effects upon the anomalous pigment.[2] Protanomalous observers possess an anomalous pigment, together with normal chorolabe; deuteranomalous observers possess an anomalous pigment, together with normal erythrolabe.[3–6]

Much work has been devoted to the determination of the spectral sensitivities of these pigments. The fine tolerance with which any spectral light can be matched to a combination of two or three fixed primaries has favored the use of color matches as a basis for precise estimates of the spectral sensitivities. But the color-matching data alone are not sufficient. If, for example, monochromatic lights from the spectral region between red and green are matched to mixtures of red and green primaries, each pigment will be excited to some extent by both the red and the green primaries, so that for each pigment the total excitation will be proportional to their weighted sum, the amount of each primary being weighted by the sensitivity of the pigment to that primary. To determine the sensitivity of the pigment to the various wavelengths matched, these primary sensitivities must be known.

This ambiguity is absent from the color matches of the red–green blind, who require only one primary to match lights in the red–green spectral range. Consequently, most determinations of the spectral sensitivities of normal color vision have been based upon data from dichromatic rather than from normal trichromatic observers. The linking hypothesis has usually been that each class of dichromat differs from normal simply by the absence of one of the normal pigments—thus that protanopes possess only chlorolabe along with the blue-sensitive pigment, deuteranopes only erythrolabe. Unfortunately, investigations of normal vision have not given unqualified support to this pigment-loss hypothesis. Many investigators have analyzed the color apparatus of the normal eye by attributing the changes of color appearance[7–11] or of incremental sensitivity[12,13] that are provoked by exposure to colored conditioning lights, to independent modifications of the sensitivities of a limited number of spectrally selective visual mechanisms, and the relative sensitivities to red and green inferred for these mechanisms (especially the red-sensitive mechanism) have frequently differed from those obtained from the red–green blind[14–19] (Table I). Many successful theoretical treatments of normal color vision[12,20–25] have assumed for the red-sensitive mechanism a spectral sensitivity different from that of the deuteranope. This evidence from normal vision by no means excludes the pigment-loss hypothesis; the significant mechanisms of normal

TABLE I. Red- and green-sensitive mechanisms in normal and dichromatic observers: ratio of sensitivity at 650 nm to sensitivity at 530 nm.

Dichromat			Normal		
Investigator	P^a	D^b	Investigator	P^a	D^b
Pitt (luminosities)	0.013	0.17	Wright	0.007	0.29
Judd (Pitt copoint)	0.014	0.15	Walters	0.016	0.35
Hsia and Graham	0.017	0.19	Stiles	0.037	0.27
Nuberg and Yustova	0.015	0.24	de Vries	0.005	0.38
Lobanova and Rautian	0.017	0.20	MacAdam	0.014	0.24
Nimeroff (Pitt copoint)	...	0.18	Fedorov	0.057	0.54
Nimeroff	...	0.22			

[a] *P:* protanope, or green-sensitive mechanism.
[b] *D:* deuteranope, or red-sensitive mechanism.

vision may not correspond to single cone pigments. Yet, recent studies of red–green blindness have also cast doubt on the loss hypothesis[26–28] (though others support it[29–32]).

The approach to be adopted here makes it possible to estimate the spectral sensitivities of normal and defective vision without commitment to the pigment-loss hypothesis of dichromacy. We proceed by comparing the different matches of normal and anomalous trichromats that both possess the pigment under consideration. A deuteranomalous observer requires more green (and less red) to match a monochromatic yellow than does a normal observer; but for both types of observer, the number of quanta absorbed by erythrolabe must be the same on both sides of the matching field. The normal and anomalous red–green mixtures must therefore be indistinguishable by erythrolabe, the excess of green in the deuteranomalous match being exactly compensated by the deficit of red. This allows a determination of the relative sensitivity of erythrolabe to the red and green primaries. Normal observers may similarly be compared with protanomalous observers, who share chlorolabe. For both erythrolabe and chlorolabe, then, the different matches of normal and anomalous observers who share the pigment in question uniquely determine the relative sensitivity of that pigment for all lights that can be matched to a mixture of red and green primaries. That is the principle of the following analysis.

NORMAL PIGMENTS

Suppose that unit energy of wavelength λ is matched to a mixture of red and green primaries, first by a normal observer and then by a protanomalous observer. Denote the energies of the red primary in the chosen mixtures by R_n for the normal match and R_p for the protanomalous match, and the energies of the green by G_n for the normal match and G_p for the protanomalous match. The sensitivity of a pigment may be defined by the number of molecules excited (which corresponds to the number of quanta absorbed) when a light of unit energy is incident on the eye. Denote the relative sensitivities of chlorolabe for the red primary by S_R, for the green primary by S_G, and for wavelength λ by S_λ.

For the normal observer, the excitation of chlorolabe (in arbitrary units) is S_λ from the unit-energy monochromatic stimulus and $(S_G G_n + S_R R_n)$ from the matching mixture of primaries. The indistinguishable visual effects imply equal excitations, so

$$S_\lambda = S_G G_n + S_R R_n. \tag{1}$$

Similarly, for the protanomalous match,

$$S_\lambda = S_G G_p + S_R R_p. \tag{2}$$

Hence,

$$S_G(G_n - G_p) = S_R(R_p - R_n), \tag{3}$$

the greater amount of red in the protanomalous match being balanced in this equation by the smaller requirement of green. Since G_n, G_p, R_n, and R_p (the energies of red and green in the protanomalous and normal matches) are known, Eq. (3) can be solved for S_R/S_G.

The spectral sensitivity of chlorolabe could then be found by referring to the color-mixture data of either the normal or the protanomalous observer, but we have preferred to derive a single estimate from the two sets of data. Elimination of either S_R or S_G between Eqs. (1) and (2) gives, respectively,

$$S_\lambda/S_G = (R_n G_p - R_p G_n)/(R_n - R_p), \tag{4}$$

$$S_\lambda/S_R = (R_n G_p - R_p G_n)/(G_p - G_n). \tag{5}$$

The quantities on the right-hand sides of these equations are known from the color-matching data, so each equation gives an estimate of the relative spectral sensitivity of chlorolabe. A similar analysis yields the spectral sensitivity of erythrolabe if R_p and G_p (the energies of red and green in the protanomalous matches) are replaced in the equations by R_d and G_d, the corresponding quantities for the deuteranomalous matches.

The results of these manipulations would be meaningless if the observers compared did not in fact possess a pigment in common. Fortunately, Eqs. (1) and (2) allow a test of this hypothesis. The right-hand side of Eq. (1), regarded as a function of λ, is the spectral sensitivity of a possible normal pigment, compatible with normal color matching. Equation (2) similarly specifies the spectral sensitivity of a possible protanomalous pigment. The ratio of the sensitivities is $[G_n + (S_R/S_G)R_n]/[G_p + (S_R/S_G)R_p]$, which we will call k_λ. If (as we have assumed) normal and anomalous observers share a pigment, it follows that when S_R/S_G is set equal to the ratio of the red and green sensitivities of the common pigment, we must have $k_\lambda = 1$ for all λ.

APPLICATION OF THE ANALYSIS

Color-matching data have been tabulated for protanomalous observers by McKeon and Wright[33] and for deuteranomalous observers by Nelson.[34] Within each of these groups, certain observers can be identified who have good wavelength discrimination and are therefore "simple protanomalous" (McKeon and Wright, observers A through F) or "simple deuteranomalous" (Nelson, observers A, D, and F). The tables given by these authors show the luminosities of the primaries required to match an equal-energy spectrum. To obtain the energies for a particular observer, we divided each primary luminosity by the luminosity required by that observer to match a stimulus of the standard energy that had the same spectral composition as the primary stimulus. However, the amounts of red in the protanomalous matches could not be treated in this way, owing to the inadequate precision of the tabulated values for matches with red lights; instead,

the red-primary luminosities were averaged for all of the protanomalous observers and the averages were divided by 0.013, a value suggested by McKeon and Wright's average protanomalous luminosity curve.

Corresponding data for normal observers were obtained from the 1931 CIE tristimulus values by applying a linear transformation from the CIE $(\bar{x},\bar{y},\bar{z})$ system to the experimental primaries of 530 and 650 nm with which the anomalous observers made their matches. We will consider only matches for wavelengths greater than or equal to 530 nm. For these wavelengths, no anomalous observer ever required any desaturating blue primary, and the amounts of blue required by the normal observers were too small to alter significantly the excitation of erythrolabe and chlorolabe.

Estimates of S_R/S_G for erythrolabe and chlorolabe have been derived from the matches made by the three types of observer at $\lambda=590$ nm. For chlorolabe, $S_R/S_G=0.0160$; for erythrolabe, $S_R/S_G=0.200$.

Figure 1 shows the spectral sensitivities of chlorolabe and erythrolabe, derived from Eqs. (4) and (5), respectively, using these values of S_R/S_G. Figure 1(a) shows the pigment common to the normal and protan; Fig. 1(b) shows the pigment common to the normal and deutan. There are two estimates for each pigment, and the curves through the points are appropriate linear combinations of the 1931 CIE tristimulus values. The estimates from Eq. (5) are unreliable for wavelengths up to 570 nm, and the estimates from Eq. (4) are unreliable beyond 630 nm. Figure 1 shows that the two estimates for each pigment agree well over the range of wavelengths within which both are reliable. The consistency of the two estimates for each pigment supports the assumption that each type of anomalous observer has a pigment in common with the normal observer. Nor do the obtained values of k_λ shown below each spectral sensitivity curve discredit that assumption, for in only one case does k_λ differ by more than 0.05 log units from the predicted value of 1.0. The vertical bars associated with each value of k_λ give the error ($\pm 2\times$S.E.) to be expected from the observed variation among the protanomalous [Fig. 1(a)] or deuteranomalous [Fig. 1(b)] observers. This variation, together with neglected sources of error—variability among normal observers, and photometric errors—could easily be responsible for the small observed deviations from $k_\lambda=1.0$. It appears, then, that protanomalous observers do share with normal observers a pigment, chlorolabe, with the spectral sensitivity shown in Fig. 1(a), and that deuteranomalous observers share with normals erythrolabe, which has the spectral sensitivity shown in Fig. 1(b).

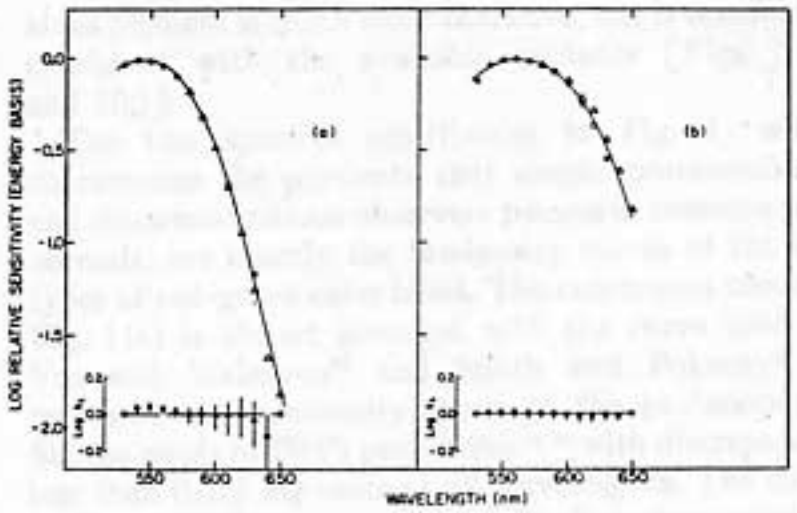

FIG. 1. Estimated spectral sensitivity of the two normal pigments sensitive in the red-green range. Triangles plot $\log S_\lambda$ from Eq. (4), circles from Eq. (5). Inset is $\log k_\lambda \pm 2\times$S.E. (a) The pigment shared with simple protanomalous observers. The curve is $S_\lambda=-\bar{x}_\lambda+3\bar{y}_\lambda$, where $\bar{x}_\lambda$ and $\bar{y}_\lambda$ are the 1931 CIE tristimulus values for an equal-energy spectrum. (b) The pigment shared with deuteranomalous observers. The curve is $S_\lambda=\bar{x}_\lambda+6\bar{y}_\lambda$.

A SINGLE ANOMALOUS PIGMENT?

A plausible conjecture is that protanomalous and deuteranomalous vision may be related in the same way as normal and anomalous vision. Schouten (cited by de Vries[35]) long ago suggested that the anomalous pigments in protans and in deutans are identical—a single pigment common to both types of anomalous vision. This hypothesis may be tested by substituting R_d and G_d for R_n and G_n in Eqs. (1)–(5). The matching data of protans and deutans at $\lambda=590$ nm yield a value of $S_R/S_G=0.0360$ for the relative sensitivity to red (650 nm) and green (530 nm) of the hypothetical single anomalous pigment. The obtained values of k_λ are shown in Fig. 2. The deviations from $k_\lambda=1.0$ are again small at all wavelengths (less than 0.1 log units) and are not large enough to exclude the single-pigment hypothesis, particularly as the results compared are from separate investigations, so that photometric errors might be responsible for small discrepancies. Moreover, the anomalous pigment is probably housed in the red-responding cones of protans but in the green-responding cones of deutans; this could perhaps account for small differences between the relative sensitivities of the pigment in protan and deutan.[36]

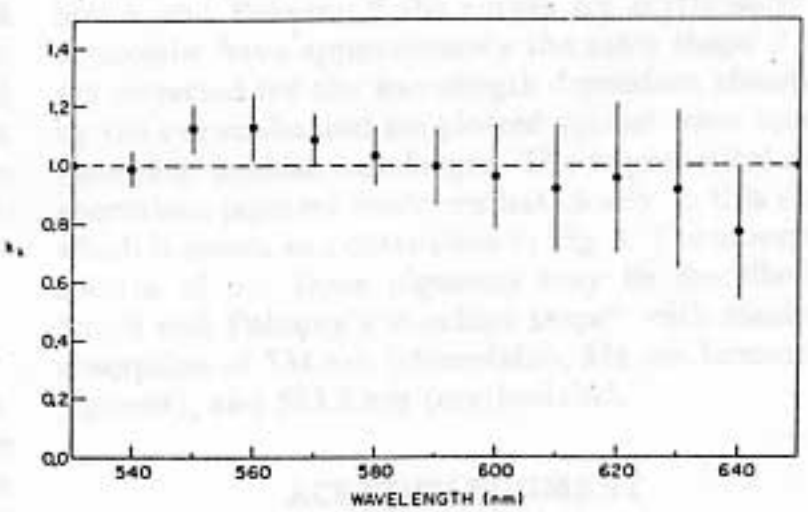

FIG. 2. Values of k_λ (linear scale) for the comparison between deuteranomalous and protanomalous matches. The vertical bars subtend plus and minus twice the standard error of the estimates.

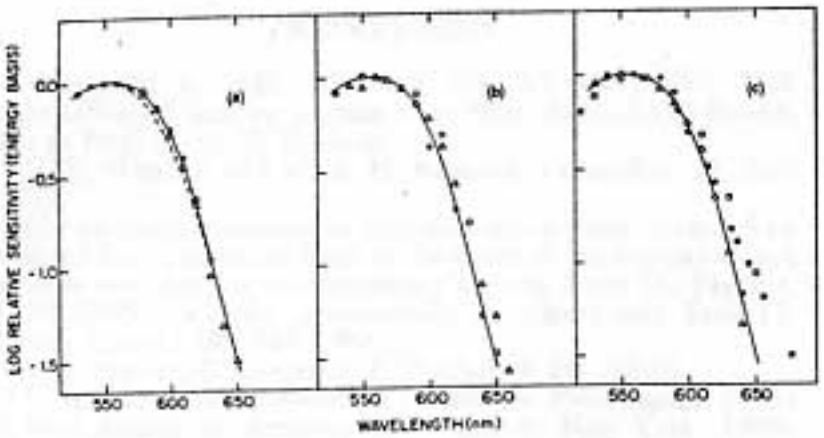

FIG. 3. (a) Estimated spectral sensitivity of the pigment common to deuteranomalous and protanomalous observers. Triangles from Eq. (4), circles from Eq. (5). The continuous curve was drawn freely to fit the points. The dotted curve (largely superimposed on the continuous curve) is an example of Smith and Pokorny's standard shape (Ref. 43), suitably positioned on a wave-number abscissa before transforming to a wavelength plot. (b) and (c): The continuous curve from Fig. 3(a), compared with experimental estimates for the anomalous pigment of the protanomalous observer (b) and of the deuteranomalous observer (c). △ Lobanova and Speranskaya (Ref. 37); ■ Walraven, van Hout, and Leebeek (Ref. 38); □ Alpern and Torii (Ref. 39); ○ Rushton, Powell, and White (Ref. 40).

Of course, the fact that the predictions made for k_λ are approximately fulfilled in Fig. 2 cannot be regarded as definite confirmation that protans and deutans have the same anomalous pigment; very different spectral sensitivities are also consistent with the data for each type of observer. Figure 2 shows only that the matching data do not exclude the common-pigment hypothesis. But if there is indeed just one anomalous pigment, it must have the spectral sensitivity shown in Fig. 3(a), where circles indicate the estimates of S_λ from the protan–deutan equivalent of Eq. (4) and triangles indicate the estimates from Eq. (5).

The continuous theoretical curve from Fig. 3(a) is reproduced in Figs. 3(b) and 3(c), where it is seen to agree well with recent experimental estimates of the spectral sensitivities of the anomalous pigments in protons and deutans, respectively.[37–40] The estimates from Alpern and Torii[39] are based upon the line-element theory of Stiles[12]; using Schrödinger's line element,[21] they generated another pair of curves that are displaced slightly toward longer wavelengths, but which again show approximate agreement between protan and deutan. Piantanida and Sperling[41] report a protan function similar to those in Fig. 3(b), but their deutan function is much flatter than any of those in Fig. 3(c). With this exception, the experimental data seem to support the single-pigment hypothesis.

DISCUSSION

These results favor the view that normal, protanomalous, and deuteranomalous vision represent the three possible pairings of three visual pigments sensitive in the red–green spectral range. The closely related observations of Mitchell and Rushton[6] firmly support this conception of the relation between normal and anomalous vision. The identification of a single anomalous pigment is much more tentative, but is reasonably consistent with the available evidence [Figs. 3(b) and 3(c)].

The two spectral sensitivities in Fig. 1, which characterize the pigments that simple protanomalous and deuteranomalous observers possess in common with normals, are exactly the luminosity curves of the two types of red–green color blind. The continuous curve in Fig. 1(a) is almost identical with the curve used by Vos and Walraven[42] and Smith and Pokorny[43] to represent the luminosity curve of the protanope; it fits the result of Pitt's protanopes[14,44] with discrepancies less than 0.025 log units at all wavelengths. The curve in Fig. 1(b) fits the results of Pitt's deuteranopes[14,44] with discrepancies less than 0.012 log units; it is very similar to Smith and Pokorny's deuteranopic curve, but is formed by a linear combination of the 1931 CIE tristimulus values for an equal-energy spectrum. This coincidence of trichromatic and dichromatic spectral sensitivities supports the pigment-loss hypothesis of dichromacy. In particular, the sensitivity to green light of the pigment common to normal and simple deuteranomalous observers (Rushton's erythrolabe) is sufficient to account for the deuteranope's almost-normal sensitivity at these wavelengths; it is unnecessary to suppose that the deuteranopic eye contains chlorolabe as well.

Among the many relevant investigations of normal vision (such as those listed in Table I), several have yielded spectral sensitivities that approximately coincide with that of chlorolabe in Fig. 1(a); Stiles's π_4' (Ref. 44) agrees to within 0.03 log units. The erythrolabe spectral sensitivity [Fig. 1(b)] has not been accurately reproduced in studies of normal vision at moderate luminances, but may be characteristic of the artificial monochromacy that follows exposure to a green light of luminance sufficient to bleach a large fraction of the visual pigment.[45,46]

None of the three pigments exhibited in Figs. 1 and 3 conforms to Dartnall's standard shape[47] for visual pigments but, like the spectral-sensitivity curves of Smith and Pokorny,[43] the curves for erythrolabe and chlorolabe have approximately the same shape if they are corrected for the wavelength-dependent absorption by the eye media and are plotted against wave number instead of against wavelength. The hypothetical single anomalous pigment conforms less closely to this shape, which is shown as a dotted line in Fig. 3. The absorption spectra of our three pigments may be described by Smith and Pokorny's standard shape[43] with maximum absorption at 534 nm (chlorolabe), 544 nm (anomalous pigment), and 555.5 nm (erythrolabe).

ACKNOWLEDGMENT

This analysis was prompted by an idea of Prof. Rushton's, who also suggested improvements in the manuscript.

REFERENCES

* Supported by AEC Contract No. AT-(40-1)-2690, NSF Grant GU-2612, and by a grant from NIH (1R01-EY00-684-03-VIS) to Prof. W. A. H. Rushton.

[1] D. E. Mitchell and W. A. H. Rushton, Vision Res. **11**, 1033 (1971).

[2] The alternative possibility that anomalous vision is caused by a colored filter present in front of the cones of the anomalous eye has been excluded for deuteranomaly by von Kries [Z. Psychol. **19**, 63 (1899)] and for protanomaly by Alpern and Torii [J. Physiol. (Lond.) **198**, 549 (1968)].

[3] A. König and C. Dieterici, Z. Psychol. **4**, 241 (1893).

[4] J. von Kries, in *Helmholtz's Treatise on Physiological Optics* (Optical Society of America, 1924; Dover, New York, 1962), Vol. II, p. 409.

[5] F. H. G. Pitt, Doc. Ophthalmol. **3**, 307 (1949).

[6] D. E. Mitchell and W. A. H. Rushton, Vision Res. **11**, 1045 (1971).

[7] J. von Kries, in *Sources of Color Science*, edited by D. L. MacAdam (The MIT Press, Cambridge, Mass., 1970), p. 109.

[8] W. D. Wright, Proc. Roy. Soc. B **115**, 49 (1934).

[9] H. V. Walters, Proc. Roy. Soc. B **131**, 27 (1942).

[10] D. L. MacAdam, J. Opt. Soc. Am. **46**, 500 (1956).

[11] N. T. Fedorov, in *Visual Problems of Colour* (H.M.S.O., London, 1958), p. 297.

[12] W. S. Stiles, Proc. Phys. Soc. Lond. **58**, 41 (1946).

[13] H. de Vries, J. Opt. Soc. Am. **36**, 121 (1946).

[14] F. H. G. Pitt, Medical Research Council Special Report No. 200 (1935).

[15] D. B. Judd, J. Opt. Soc. Am. **35**, 199 (1945).

[16] Y. Hsia and C. H. Graham, Proc. Natl. Acad. Sci. USA **43**, 1011 (1957).

[17] N. D. Nuberg and E. N. Yustova, in *Visual Problems of Colour* (H.M.S.O., London, 1958), p. 475.

[18] N. V. Lobanova and G. N. Rautian, Dokl. Akad. Nauk SSR **146**, 1193 (1962) [Sov. Phys.—Dokl. **7**, 949 (1962)].

[19] I. Nimeroff, J. Opt. Soc. Am. **60**, 966 (1970).

[20] H. von Helmholtz, *Handbuch der Physiologischen Optik, 2nd ed.* (Voss, Hamburg, 1896), Vol. II.

[21] E. Schrödinger, in *Sources of Color Science*, edited by D. L. MacAdam (The MIT Press, Cambridge, Mass., 1970), p. 134.

[22] D. L. MacAdam, in *Visual Problems of Colour* (H.M.S.O., London, 1958), p. 577.

[23] R. M. Boynton, J. Opt. Soc. Am. **50**, 929 (1960).

[24] H. G. Sperling, Vision Res. **1**, 42 (1961).

[25] P. L. Walraven, Thesis (Utrecht, 1962).

[26] D. Farnsworth, Vision Res. **1**, 1 (1961).

[27] H. Scheibner and R. M. Boynton, J. Opt. Soc. Am. **58**, 1151 (1968).

[28] R. D. Watkins, Vision Res. **9**, 1185 (1969).

[29] R. G. Speelman and J. Krauskopf, J. Opt. Soc. Am. **53**, 1103 (1963).

[30] W. A. H. Rushton, Nature **206**, 1087 (1965).

[31] H. D. Baker and W. A. H. Rushton, J. Physiol. (Lond.) **176**, 56 (1965).

[32] S. S. Miller, J. Physiol. (Lond) **223**, 89 (1972).

[33] W. M. McKeon and W. D. Wright, Proc. Phys. Soc. Lond. **52**, 464 (1940).

[34] J. H. Nelson, Proc. Phys. Soc. Lond. **50**, 661 (1938).

[35] H. de Vries, Physica (Utr.) **14**, 367 (1948).

[36] A. W. Snyder and P. A. V. Hall, Nature **223**, 526 (1969).

[37] N. V. Lobanova and N. I. Speranskaya, Biophysics **6**, 668 (1961).

[38] P. L. Walraven, J. M. J. van Hout, and H. J. Leebeek, J. Opt. Soc. Am. **56**, 125 (1966).

[39] M. Alpern and S. Torii, J. Gen. Physiol. **52**, 717 (1968); J. Gen. Physiol. **52**, 738 (1968).

[40] W. A. H. Rushton, D. S. Powell, and K. D. White, Vision Res. **13**, 2017 (1973).

[41] T. Piantanida and H. G. Sperling, Vision Res. **13**, 2033 (1973); Vision Res. **13**, 2049 (1973).

[42] J. J. Vos and P. L. Walraven, Vision Res. **11**, 799 (1971).

[43] V. C. Smith and J. Pokorny, Vision Res. **12**, 2059 (1972); J. Pokorny, V. C. Smith, and I. Katz, J. Opt. Soc. Am. **63**, 232 (1973).

[44] G. Wyszecki and W. S. Stiles, *Color Science* (Wiley, New York, 1967).

[45] N. T. Fedorov and V. Fedorova, Naturwissenschaften **16**, 757 (1928).

[46] G. S. Brindley, J. Physiol (Lond.) **122**, 332 (1953).

[47] H. J. A. Dartnall, *The Visual Pigments* (Methuen, London, 1957).