$m_{\mu}$  (34). It should be clear from Fig. 8 that a fused B-G mechanism would cross the R curve, or a fused B-Rmechanism would cross the G curve, near these wavelengths.

The synchromias include not only limiting types such as those already discussed, but also intermediate conditions in which, though three visual pigments excite only two sensory channels, their proportions depart considerably from the average. These are the anomalous dichromats, just as trichromats in whom the distribution of color sensitivities departs widely from the average are the anomalous trichromats. They probably include all intergradations between the synchromias with normal luminosity function and the achromias. They appear nevertheless to form a minor category. Thus the "deuteranopes" of Figs. 12 and 13 include all those worked on by the authors cited, except for two intermediates measured by Hsia and Graham, and an unspecified few of Willmer's subjects.

## **References and Notes**

- T. Young, *Phil. Trans. Roy. Soc. London* 1802, 12 (1802); *Lectures in Natural Philoso-phy* (London, 1807), vol. 1, p. 440; vol. 2, p. 613.
- 1a. Lectures in Natural Philosophy
- (London, 1807), vol. 2, p. 315. H. von Helmholtz, Ann. Physik. 87, 45 (1852); translation, Phil. Mag. ser. 4, 4, 519 2 H (1852)
- Maxwell, Proc. Roy. Inst. Gt. Brit. 6, 3. j 260 (1871).
- 260 (1871).
  ..., Scientific Papers (Cambridge, 1890), vol. 1, p. 410; vol. 2, p. 267.
  M. Schultze, Arch. Mikr, Anat. 2, 175 (1866).
  For the history of color vision investigations and critical discussions of the data and theories, I am indebted to the following

sources: G. S. Brindley, *Physiology of the Retina and Visual Pathway* (Arnold, London, 1960), chap. 7; C. H. Graham, "Color theory," in *Psychology: A Study of a Science*, 5. Koch Ed. (McCraw Will), New York S. Koch, Ed. (McGraw-Hill, New York, 1959), vol. 1, p. 145; Y. le Grand, Light, Colour and Vision (Chapman and Hall, Colour and Vision (Chapman and Fam, London, 1957); S. Hecht, J. Opt. Soc. Am. 20, 231 (1930); G. L. Walls and R. W. Mathews, "New Means of Studying Color Blindness and Normal Foveal Vision," Univ. Calif. Berkeley Publ. Psychol. 7, No. 1 (1952).

- Stiles, Ned. Tijdschr. Natuurk. 15, 7. W. 125 (1949).
- , Proc. Natl. Acad. Sci. U.S. 45, 100 8. (1959).
- (1959). 9. P. K. Brown and G. Wald, *Nature* **200**, 37 (1963). 10. W. B. Marks, W. H. Dobelle, E. F. Mac-10. Nichol, Jr., Science 143, 1181 (1964); P. K. Brown and G. Wald, *ibid*. 144, 45 (1964). G. Wald, Federation Proc. 22, no. 2, 519
- 11. G (1963).
- 12. E. Auerbach and G. Wald, Science 120, 401
- E. Auerbach and G. Wald, Science 120, 401 (1954).
   G. S. Brindley, J. Physiol. London 122, 332 (1953); E. N. Willmer, Doc. Ophthalmol. 9, 235 (1955).
- 235 (1955).
  14. Y. Hsia and C. H. Graham, Proc. Natl. Acad. Sci. U.S. 43, 1011 (1957).
  15. The troland, a unit of retinal illumination, is the luminance in candelas/m<sup>2</sup> multiplied by the trolande". The trolande and the set for fact in a transfer of the set o Proc. Natl.
- is the luminance in candelas/m<sup>2</sup> multiplied by the pupil area in m<sup>2</sup>. For "effective trolands" the latter is corrected for the Stiles-Craw-ford effect. Cf. Y. le Grand (6), p. 104. E. Ludvigh and E. F. McCarthy, Arch. Ophthalmol. 20, 37 (1938). E. A. Boettner and J. R. Wolter, Invest. Ophthalmol. 1, 776 (1962). I am indebted to these outbook for a pupperiod transcript of 16. E.
- 17. E
- these authors for a numerical transcript of portions of their data.
- 18. G. Wald and P. K. Brown, Science 127, 222
- G. Wald and P. K. Brown, Science 127, 222 (1958).
   W. W. Coblentz and W. B. Emerson, Bull. Bur. Std. U.S. 14, 167 (1918–19); K. S. Gibson and E. P. T. Tyndall, Sci. Paper Natl. Bur. Std. U.S. 19, 131 (1923); P. Jainski, Dissn. Tech. Hochsch., Berlin (1938); N. T. Federov, V. I. Federova, A. G. Plakhov, L. O. Seletzkaya, J. Phys. Acad. Sci. U.S.S.R. 3, 5 (1940); E. P. Hyde and W. E. Forsythe, Astrophys. J. 42, 285 (1915).
   G. Wald, Science 101, 653 (1945); Doc. Ophthalmol. 3, 94 (1949).
   E. Auerbach and G. Wald, Am. J. Ophthal-
- E. Auerbach and G. Wald, Am. J. Ophthal-mol. 39, 24 (1955).
   R. A. Weale, J. Physiol., London 119, 170
- (1953).
- (1953).
  23. G. Wald, "Retinal chemistry and the physiology of vision," in Visual Problems of Colour, Natl. Phys. Lab., Gt. Brit. Proc. Symp. 8, (1958), vol. 1, p. 7; H. J. A. Dart-

nall, The Visual Pigments (Methuen, London, 1957); "The identity and distribution of vis-ual pigments in the animal kingdom," in The Eye, H. Davson, Ed. (Academic Press, New York, 1962), vol. 2, p. 367. F. H. G. Pitt, Proc. Roy. Soc. London B132, 101 (1944)

- 24. 101 (1944). 25
- W. A. H. Rushton and R. D. Cohen, *Nature* **173**, 301 (1954); G. Wald, *Science* **119**, 887 (1954)
- (1954).
   W. A. H. Rushton, Progr. Biophys., Biophys. Chem. 9, 240 (1959).
   R. A. Weale, Opt. Acta 6, 158 (1959).
   W. A. H. Rushton, J. Opt. Soc. Amer. 54, COMMUNICATION (1964).
- 273 (1964).
- ..., J. Physiol., London 168, 345 (1963). ..., ibid., p. 360. ..., ibid. 169, 31P (1963). 29 30
- , *ibid.* 109, 317 (1963).
   H. D. Baker and W. A. H. Rushton, *ibid.*, 91P (1963).
   J. C. Maxwell, in G. Wilson, *Researches on Colour-Blindness* (Sutherland and Knox, Nutrie 1005).

- J. C. Maxwell, in G. Wilson, Researches on Colour-Blindness (Sutherland and Knox, Edinburgh, 1855), p. 153.
   D. B. Judd, J. Opt. Soc. Am. 33, 294 (1943).
   ......, *ibid.* 35, 199 (1945).
   A. Fick, "Die Lehre von der Lichtempfin-dung," in Handbuch der Physiologie, L. Her-mann, Ed. (Leipzig, 1879), vol. 3, pt. 1, p. 130 139.
- von Kries, "Die Gesichtsempfindungen," 37. J. von Kries, "Die Gesichtsempfindungen," in Handbuch der Physiologie des Menschen, W. Nagel, Ed. (Vieweg, Braunschweig, 1905), vol. 3, p. 109; also in H. von Helmholtz, Treatise on Physiological Optics, Southall, Ed. (Optical Society of America, Washington, 1924), vol. 2, p. 402: "The writer suggests the names protanopes and deuteranopes to describe the two kinds of dichromats, that is, persons who lack the first component or the second component, respectively, of the norsecond component, respectively, of the normal visual organ."
  38. D. B. Judd, J. Opt. Soc. Am. 39, 252 (1949).
  39. E. N. Willmer, Doc. Ophthalmol. 9, 235 (1955)
- (1955).
- (1955).
  40. F. H. G. Pitt, "Characteristics of dichromatic vision," Med. Res. Council Spec. Rept., No. 200, H.M. Stat. Office, London (1935).
  41. I thank C. H. Graham and E. N. Willmer for making their individual measurements available to me.
  42. W. D. Wright, J. Opt. Soc. Am. 42, 509 (1952).
- W. D. Wright, J. Opt. Soc. Am. 42, 509 (1952).
   C. H. Graham, H. G. Sperling, Y. Hsia, A. H. Coulson, J. Psychol. 51, 3 (1961).
   Supported in part with grants from the Na-
- tional Science Foundation and the U.S. Office of Naval Research. I thank the members of the Zoology Department, Cambridge Univer-sity, and C. F. A. Pantin for their hospitality. I am indebted also to my wife, Ruth Hub-bard, and to Dana Gedmintas, Alexander Hoffman, and L. E. R. Picken for serving as subjects in these experiments.

## Appendix by W. S. Stiles: Foveal Threshold Sensitivity on Fields of Different Colors

George Wald's interesting measurements of increment thresholds by the two-color threshold method (1) are closely related to results I obtained in a comparable study, of which only certain salient features were published (2, 3). Wald kindly expressed a wish to refer to my data on the variation of the increment threshold with

test wavelength when the retina is adapted to steady fields of different colors and brightness-the latter being generally lower than those Wald has used. These data (mean results) are summarized in Fig. 1, which shows curves for the 13 field conditions used. Each curve represents the variation of the logarithm of the reciprocal of the increment threshold, log  $(1/N_{\lambda})$ , with the wave number of the test stimulus,  $1/\lambda$ . To compress the curves into a single figure, a conveniently chosen constant (C), has been added to the values for each curve (see Fig. 1), so that the positions of the curves along the ordinate axis are significant only when allowance is made for C. The essential details of the measurement conditions are as follows

The test stimulus was a circular light, 1 degree in diameter, that was flashed for 0.2 second once every 3 seconds. It was observed by monocular foveal vision, and each threshold was deter-

The author, formerly on the staff of the National Physical Laboratory, Teddington, England, now resides at 89 Richmond Hill Court, Richmond, Surrey.

mined from a frequency-of-seeing curve as the test intensity for a 50 percent chance of seeing. The adapting field was monochromatic, of wavelength  $\mu$ , 10 degrees in diameter, with quantum intensity  $M_{\mu}$ . Both  $M_{\mu}$  and  $N_{\lambda}$  are

22.500

expressed as the number of quanta per second entering the eye per square degree of adapting field or of test stimulus. Maxwellian view was used, with a virtual artificial pupil smaller than the eye pupil. For the adapting field

15.000

17,500

the corresponding troland brightness,  $(T)_{\mu}$ , is obtained with the conversion formula:

og 
$$T_{\mu} = \log M_{\mu} + \log 1/\mu + \log V_{\mu} + \frac{11.651}{11.651}$$
,  
where  $V_{\mu}$  is the relative luminous ef-

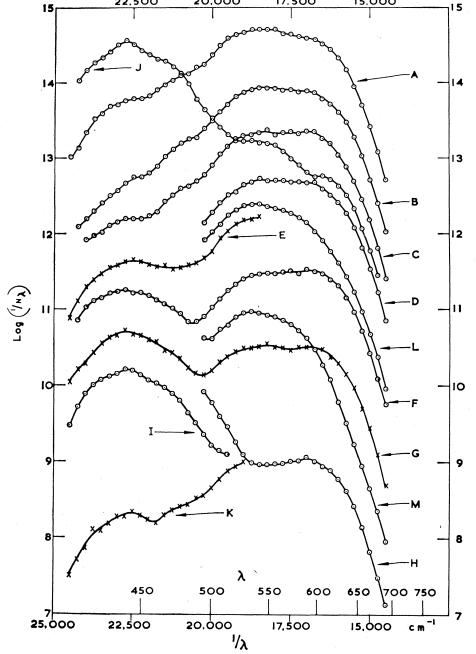
ficiency function, at wavelength  $\mu$ , of the Commission Internationale de l'Eclairage (4). Four subjects were used in making these measurements (Fig. 1).

Because of the close spacing of the test wave numbers used, the curve for the complete test spectrum with a given field could not be measured in one session. Therefore, determinations were made, independently, of the curve for a range of longer wavelengths  $(1/\lambda =$ 20250 cm<sup>-1</sup> to the red end) or for a range of shorter wavelengths  $(1/\lambda =$ 18500, 19000, or 19500 cm<sup>-1</sup> to the blue end). Each subject made four, and in some cases eight, determinations of the curve for the shorter or longer wavelength range on different days. The mean values of log  $1/N_{\lambda}$  for each subject were computed. As the main features of the curves recur for all subjects, who differ mainly in the absolute values of the increment thresholds, the means for the subjects were averaged to obtain the results given here. Where both longer and shorter wavelength ranges were studied for substantially the same field conditions, the two mean curves were combined into a single curve by raising one section slightly and lowering the other by the same amount, so as to give on the average the same values at the test wave numbers in the overlap range (20250 to 18500, 19000 or 19500 cm<sup>-1</sup>). The shifts required were about 0.02 log unit.

Certain difficulties in interpreting curves of log  $(1/N_{\lambda})$  against  $1/\lambda$  in terms of spectral sensitivities of independent visual mechanisms (what I have called  $\pi$  mechanisms) I have already discussed (3). Wald makes some comparisons between these data and his new data, but I should like to defer further comment until the implications of recent work (5) on threshold summation have been evaluated.

## References and Notes

- G. Wald, Science, this issue.
   W. S. Stiles, Coloquio sobre problems opticos de la vision (Union Internationale de Physique Pure et Appliquée, Madrid, 1953), vol. 1,
- p. 65. 3. ——, Proc. Natl. Acad. Sci. U.S. 45, 100
- 1959.
  See, for example, Y. le Grand, Light, Colour and Vision (Wiley, New York, 1957) for definitions of the relative luminous efficiency func-
- tion and the troland unit (pp. 71 and 102). 5. R. M. Boynton, M. Ikeda, W. S. Stiles, Vision Research, in press.



20,000

Fig. 1. Spectral sensitivity of the fovea measured with test fields superimposed on steady backgrounds of various wavelengths and brightnesses. The sensitivity is expressed as the logarithm of the reciprocal of the increment threshold in quanta per second entering the eye per square degree of test field. Mean results of determinations on a dark background (A) and on backgrounds of the following wavelengths and brightnesses: (B) 434.8 m $\mu$ , 12.0 trolands; (C) 470.6 m $\mu$ , 209 trolands; (D, E, F) 500.0 m $\mu$ , 42.8, 41.4, and 1552 trolands; (G, H, I) 548.0 m $\mu$ , 203, 90200, and 2790 trolands; (J) 588.2 m $\mu$ , 19320 trolands; (K, L, M) 666.7 m $\mu$ , 26.8, 29.2, and 2506 trolands. To bring the curves into a single chart, the following plotting constant (C) was added to each: (A) 20.0; (B) 19.9; (C) 20.2; (D) 18.8; (E) 18.2; (F) 18.9; (G) 17.0; (H) 18.2; (I) 16.8; (J) 21.5; (K) 14.8; (L) 18.0; (M) 17.8. Four subjects S and F; curves E and G, averages for subjects S and K; and the remaining curves, averages for all four subjects.

4 SEPTEMBER 1964