The Receptors of Human Color Vision

Action spectra of three visual pigments in human cones account for normal color vision and color-blindness.

George Wald

"From three simple sensations, with their combinations, we obtain several primitive distinctions of colours; but the different proportions, in which they may be combined, afford a variety of tints beyond all calculation. The three simple sensations being red, green, and violet, the three binary combinations are yellow, consisting of red and green; crimson, of red and violet; and blue, of green and violet; and the seventh in order is white light, composed by all the three united.
—THOMAS YOUNG, *Lectures on Natural Philosophy,* 1807

That normal color vision involves the operation of three independent variables was first stated plainly by Thomas Young (*1*); yet it was not until this notion was embodied in the color mixture experiments and equations of Helmholtz (*2*) and Maxwell (*3, 4*) that it gained general currency. Young had expressed his idea in terms of three primary color sensations—red, green, and violet—excited by three types of retinal receptors differing in spectral sensitivity. With Max Schultze's recognition that color vision is exclusively the business of cones (*5*), this came to mean three types of cone with different spectral sensitivities. That posed, a century ago, the problem of determining what those spectral sensitivities are. It is a task that must be approached directly, since it has been clear for some time that there is no unique theoretical solution: that an infinite array of hypothetical trios of spectral sensitivity functions, all interconvertible by linear transformations, can satisfy the formal demands of most color-vision measurements (*6*). Rather than go on with such formal constructions, we need to determine the properties of the receptor mechanisms that in fact govern human color vision.

In the past Stiles has come closest to solving this problem by sensory methods (*7, 8*). Recently also we have had direct microspectrophotometric measurements of the difference spectra of the light-sensitive pigments in the human fovea (*9*), and in single parafoveal cones (*10*).

The present paper describes a further analysis of such mechanisms. I came to these experiments indirectly. Having extracted two visual pigments from a crayfish eye, I tried to learn what they were doing (*11*). It turned out that the crayfish possesses an apparatus suitable for color vision, having at least two visual pigments segregated in different receptors and poised at about the same level of sensitivity. A simple procedure was devised for analyzing these arrangements. The sensitivity throughout the spectrum was measured in the dark-adapted eye. Then, one type of receptor being selectively adapted to a colored light, a redetermination of visual thresholds throughout the spectrum revealed the spectral sensitivity of the other type of receptor. So, for example, with the eye continuously adapted to red light, the spectral sensitivity measured was that of the blue-receptor. Conversely, on adaptation to blue light one could measure the spectral sensitivity of the red-receptor. The response of each type of receptor is not at all distorted by such background adaptations. This could be shown in organisms possessing a single visual system—for example, lobsters or horseshoe crabs—in which the spectral sensitivity is identical whether measured in the dark-adapted eye or under red or blue light.

Such invariance with the conditions of adaptation is an essentially photochemical criterion, characterizing the operation of a single visual pigment. The spectral sensitivities measured in this way have the force of action spectra of visual pigments. This is not necessarily the criterion for isolating a single receptor type, for instance, a single type of cone; for a cone containing a mixture of visual pigments, or any more central photoreceptor mechanism responsive to several visual pigments, would change in spectral sensitivity with the color of the adapting light.

The experiments reported here extend this type of procedure to the human eye. In retrospect it was clear that this method is a limiting case of Stiles's two-color threshold technique (*7, 8*). As ordinarily employed this involves determining the way in which the increment threshold at one wavelength rises with the brightness of background at another wavelength. The present measurements correspond to increment thresholds measured on steady backgrounds of very high brightness. On inquiry it turned out that Stiles had made similar measurements, a short account of which he generously agreed to append to this article. Related procedures have also been used to partially isolate the spectral sensitivities of the blue-receptor (*12*) and of the green- and red-receptors (*13*).

Procedure

The experimental arrangement is shown in Fig. 1. It involves two light paths, one for monochromatic test flashes, the other for a steady, colored background radiation upon which the test flashes are superimposed. Both are seen in Maxwellian view, a field lens in each pathway focusing the light upon a fixed exit pupil. Both lenses are therefore seen as evenly illuminated, the background appearing as a circular field subtending an angle of 3.5° with the eye, the test field as a 1° circle centered upon it. Central fixation is maintained either with a luminous white fixation point for dark or dim backgrounds (made by passing light down a tapered quartz rod to appear

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as a bright point at its tip), or with a black fixation point when the background is too bright for a luminous point to be easily visible.

For the test field the light of a 100-watt zirconium arc was projected through a Bausch and Lomb grating monochromator with slits set to transmit a wave band 3.3 mμ wide throughout the spectrum. A photographic shutter set the exposure at 45 msec. The intensity was regulated by a pair of neutral wedges rotating in opposite directions so as to compensate each other, and by neutral filters.

Observations

The subject, with head held in a chin-and-forehead rest, looked through the 3.5-mm exit pupil, either at a luminous white fixation point in an otherwise dark field, or at a black point at the center of a colored background field, 3.5° in diameter. The test field was exposed for flashes of 45 msec, beginning at a subthreshold intensity, and brightened step by step until the subject reported just seeing it. Since the test field was 1° in diameter and fixated centrally, its image fell entirely within the area of the fovea, effectively 1.5° to 1.7° in diameter, which contains only cones. The data are expressed in terms of the logarithm of the relative sensitivity, the sensitivity being the reciprocal of the relative number of photons per flash needed to just see the test field. Some idea of absolute sensitivities can be gained from the fact that under the conditions of these experiments the first subject (R.H.), when dark-adapted, required about 10^4 photons per flash at 560 mμ to see the field, and the second subject (D.G.) required about 1.6 times this quantity [see also (*14*)].

Spectral sensitivities at the corneal level. Figure 2 shows measurements on the right eye of R.H., in terms of relative numbers of photons incident upon the cornea. The log sensitivity of the dark-adapted fovea is greatest at about 562 mμ, falling symmetrically to both sides except for an abrupt shoulder in the blue. This curve represents the overall sensitivity of the fovea, a composite of the spectral sensitivities of all the types of cone it contains.

To isolate the individual functions that make up this composite, background radiations of various colors and brightnesses were chosen on the basis of a priori considerations and empirical trial. It has already been noted that this procedure tends to isolate the spectral sensitivities (action spectra) of visual pigments rather than specific types of cone. To the degree that the pigments are segregated, one to a cone, it does both; but in the event that some cones contain mixtures of pigments, it would isolate only the pigments. I use such terms as blue- or red-receptor below to refer more particularly to a pigment than to the cone that contains it, and attempt to clarify these distinctions further in the discussion that follows.

When the fovea is continuously adapted to bright yellow light containing all wavelengths longer than 550 mμ [Corning filter 3482; log foot lamberts, 6.00; log effective trolands (*15*), 7.01], the spectral sensitivity curve is that of the blue-receptor. It consists of a high, narrow band, maximal at about 440 mμ. The low, broad shoulder at long wavelengths apparently is not an intrinsic part of this function but represents the residual sensitivities of other receptors.

Simultaneous adaptation to wave bands in the blue and red, and hence to purple light, isolates the green-receptor. In Fig. 2 this involves adaptation to a background radiation that includes all wavelengths shorter than 462 mμ and longer than 645 mμ (Wratten filter 35; log foot lamberts, 4.34; log effective trolands, 5.42). The spectral sensitivity is greatest at about 548 mμ and displays a broad shoulder in the blue, which is, as will appear, an extraneous effect of the ocular pigmentation.

Adaptation to blue light isolates the red-receptor. Figure 2 shows two such experiments, involving different color filters and brightnesses. The upper curve was obtained with a blue background radiation rising from 500 mμ to a peak at 430 mμ (Wrattan filter 47B; log foot lamberts, 4.27; log effective trolands, 5.35). The lower curve was measured on a background radiation rising from 530 mμ to a peak at 440 mμ (Wrattan filter 47; log foot lamberts, 5.12; log effective trolands, 6.15). Both curves show peaks at about 580 mμ and are nearly identical in shape, showing the invariance of such action spectra with the conditions of adaptation once a reasonable isolation has been achieved.

Figure 3 shows a similar analysis of the foveal sensitivities of subject D.G. The results differ only in detail from those for R.H. The spectral sensitivity of the dark-adapted fovea is maximal at about 568 mμ; and the sensitivity curves for the blue-, green-, and red-receptors show peaks at about 435, 550, and 585 mμ. The two latter curves, like that for the dark-adapted fovea, lie at slightly longer wavelengths than those for R.H.; and the curves for the dark-adapted and purple-adapted eye display only gentle in-

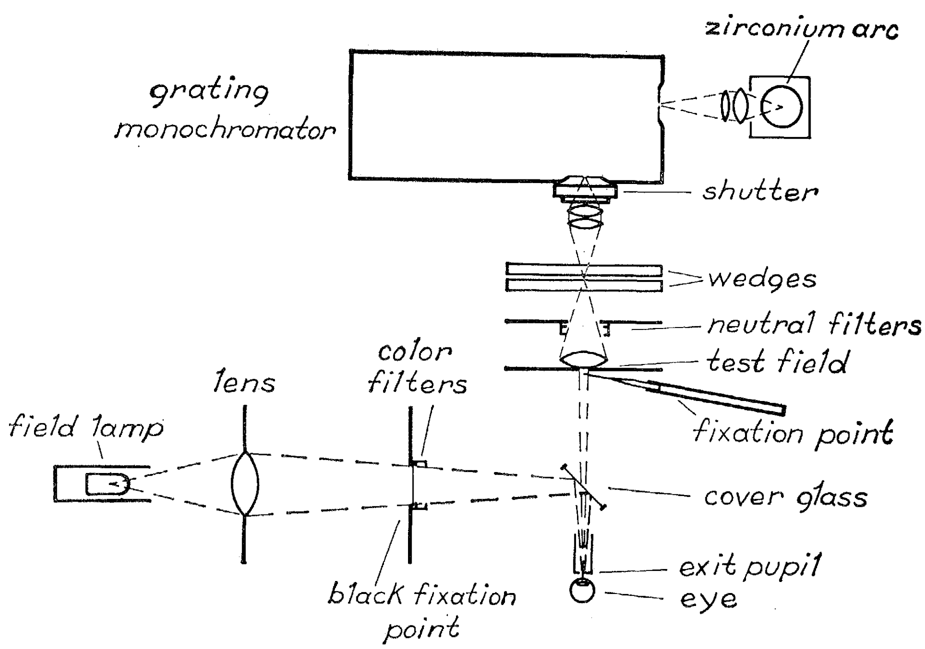


Fig. 1. Arrangement of the apparatus. It consists essentially of two light paths, one for presenting monochromatic test flashes of graded intensity, superimposed on steady colored backgrounds provided through the other light path. Both the test and background fields are seen in Maxwellian view.

flections in the blue, whereas those for R.H. have large and abrupt shoulders. The reason for these differences will appear shortly.

The isolation of individual spectral sensitivity curves by these methods involves trying numbers of filters and brightnesses. The blue-receptor is isolated rather easily, since it lies so far from the others. Separating the curves of the green- and red-receptors is more difficult since they overlap so widely, and it may be too much to expect absolute isolations. The conditions finally chosen were those that yielded the narrowest and simplest shapes of spectral sensitivity function,

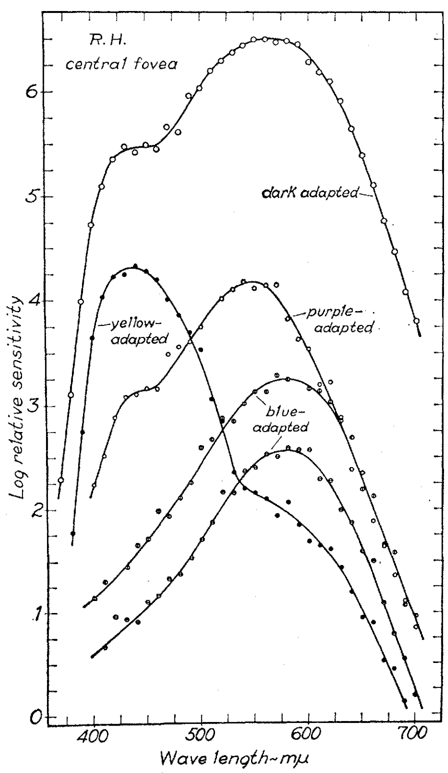


Fig. 2. Spectral sensitivities of the dark-adapted fovea and the single color-vision pigments, measured at the corneal level in R.H. The sensitivity of the total fovea is greatest at about 562 mμ (ave. of 2 experiments). Adaptation to yellow light isolates the action spectrum of the blue-sensitive pigment (λ_{max} 438 mμ); to a mixture of violet and red, hence purple light, that of the green-sensitive pigment (λ_{max} 548 mμ); and to blue light, that of the red-sensitive pigment (λ_{max} 580 mμ). The results of two different blue-adaptations demonstrate the invariance of such action spectra with the conditions of adaptation. Ordinates are log relative sensitivity (log 1/threshold), expressed in terms of relative numbers of photons per flash incident upon the cornea of the eye. Absolute sensitivities can be judged from the fact that the maximal sensitivity of the dark-adapted fovea corresponds to a threshold of about 10^4 photons.

on the assumption that these criteria should mark the most complete isolations.

We can derive some assurance that the individual receptor curves of Figs. 2 and 3 succeed in this to a degree from experiments in which they are isolated two at a time. In Fig. 4 the curves marked "red-adapted" were obtained with two brightnesses of a red background radiation containing only wavelengths longer than 630 mμ (Corning filter 2403. Upper curve: log foot lamberts, 2.60; log effective trolands, 3.77. Lower curve: log foot lamberts, 5.42; log effective trolands, 6.44). The red light having selectively adapted the red-receptor, these spectral sensitivity curves display the peaks of the blue- and green-receptors. At the lower brightness of background, the green-receptor has λ_{max} about 550 mμ, as in Fig. 2; the minor maximum of the blue-receptor is pulled toward longer wavelengths by some degree of fusion with the major band, so that it lies at about 450 mμ. Conversely, at the higher brightness the principal peak, that of the blue-receptor, lies at its proper position, 440 mμ (cf. Fig. 2), whereas the minor green-sensitivity maximum is pulled toward it, so as to lie at about 535 mμ.

Similarly (Fig. 4) a bright green background (Ilford filter 604; transmission 500-540 mμ, peaking at 520 mμ; log foot lamberts, 4.85; log effective trolands, 5.90) selectively adapts the green-receptor, so that the residual spectral-sensitivity curve displays the maxima of the blue- and red-receptors, at about 440 mμ and 585 mμ (compare Fig. 2).

The fact that the sensitivity peaks take about the same positions when in pairs as when isolated singly indicates that we are dealing with genuine properties of the receptor pigments.

Ocular and macular absorptions. Such spectral sensitivity curves, measured in terms of light incident on the surface of the cornea, govern how we see; yet relative to the intrinsic properties of the cones or visual pigments, their shapes are distorted by the filtering action of colored structures in the eye. These are principally the yellow lens and the yellow pigmentation of the macula lutea.

Figure 5 shows an estimate of the average absorbance (extinction, optical density) of the refractive structures of the human eye, prepared from the measurements of Ludvigh and McCarthy (four eyes) (*16*), Boettner and Wolter (9 eyes) (*17*), and my own comparison of the average spectral sensitivity of rod vision with the absorption spectrum of dark adapted human rods (*18*) (absorbance = log I_0/I, in which I_0 is the incident and I the transmitted intensity). Figure 5 shows also the absorption spectrum of the human macula (average of eight eyes) (*9*; also unpublished observations). Adding these together yields an estimate of the total absorbance of the ocular structures, from the corneal surface to the cones, in the human fovea. This added to the log spectral sensitivity measured at the cornea yields the spectral sensitivity at the level of the cones. Such an average correction is suitable for dealing with the averaged data from numbers of subjects. Ocular and macular pigmentations vary widely, however, and the data for individual observers require individual correction.

Individual differences in spectral sensitivity. Several years ago I prepared a curve for the average cone sensitivity ("photopic luminosity"), combining the results of a number of investigations (*19*). It includes measurements on several hundred subjects, and is

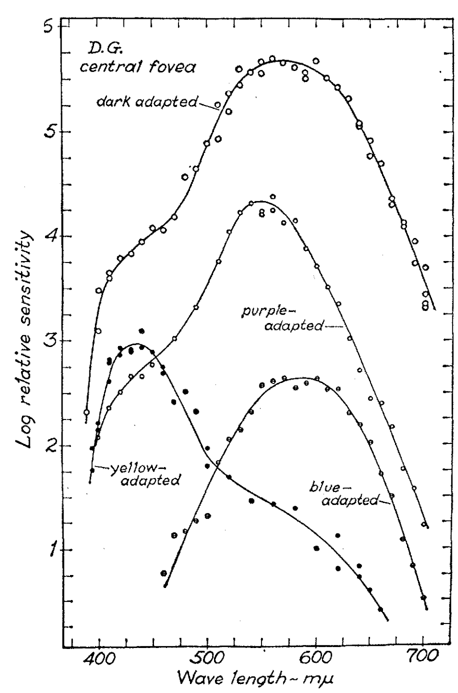


Fig. 3. Spectral sensitivities of the dark-adapted fovea and the single foveal pigments, measured at the corneal level in D.G. The foveal sensitivity is greatest at about 568 mμ where the visual threshold is about 1.6 × 10^4 photons per flash. The blue-, green-, and red-sensitive pigments display maximum sensitivities at about 435, 550, and 585 mμ. Otherwise as in Fig. 2.

highly reliable. (See the normal cone sensitivity curves in Figs. 11 to 13.)

The spectral sensitivity of R.H.'s dark-adapted fovea (Fig. 2) agrees well with this function from about 700 mμ to 480 mμ. At shorter wavelengths, however, the curve for R.H. displays a bulge of higher sensitivity, greatest at about 440 mμ, and resembling the sensitivity curve of the blue-receptor. I would conclude that R.H. possesses nearly the average ocular and macular transmissions but departs from the average subject in having a considerably higher blue-sensitivity (0.3 log unit higher, hence about twice as high at 440 mμ).

In an earlier investigation in which I was able to make measurements at only a few wavelengths, I thought that R.H.'s relatively high foveal sensitivity in the blue, like that of her brother, was caused by a lack of macular pigmentation (*20*). This sensitivity now appears in both cases to be caused by a greater than average amount of blue-receptor. We do not yet know whether this departure from the average is sufficient to categorize these subjects as color-anomalous. In any case this condition, just the opposite of blue-blindness (hence blue-richness, "hypercyanopia") appears, like color blindness, to be genetically determined.

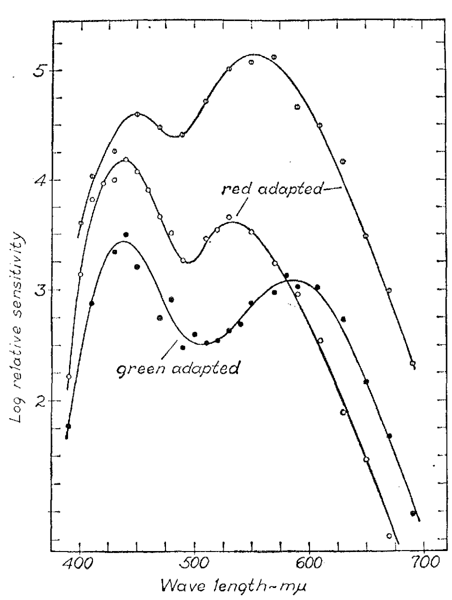


Fig. 4. Spectral sensitivities of the color-vision pigments of R.H., measured in pairs at the corneal level. Adaptation to two brightnesses of red light (wavelengths > 630 mμ) selectively adapts the red-receptor, the resultant sensitivity curves displaying in different proportions the peaks of the blue- and green-sensitive pigments, at about 440 and 550 mμ. (In each instance the minor peak is displaced toward the major peak by some degree of fusion with it.) Adaptation to green light, selectively adapting the green-sensitive pigment, exposes the peaks of the blue- and red-sensitive pigments, at about 440 and 585 mμ.

The spectral sensitivity of D.G.'s dark-adapted fovea (Fig. 3) departs from the average luminosity curve in an entirely different way. Compared with the average, D.G.'s sensitivity decreases more and more from the red to the violet. On subtracting her curve from the average function, one obtains a curve looking much like the one for total ocular and macular absorbance shown in Fig. 5. I conclude that D.G. has nearly the average distribution of color receptors, but a considerably denser ocular and macular pigmentation. Adding her departure from the photopic luminosity curve to the total ocular absorbance of Fig. 5 yields her individual correction.

These two subjects exemplify the two kinds of individual differences that underly changes in the shape of "corneal" spectral sensitivity curves even within the normal range: differences in ocular and macular transmission, and differences in the relative sensitivities of the color mechanisms. Such differences also are found within a single retina. The macular pigmentation is concentrated in the central retina, thinning out peripherally, and very dilute or absent beyond 5° from the fovea. The proportions of the color receptors may change also from the center to the periphery. In some subjects the far periphery behaves as though red-blind (*3*, p. 279; *12, 21*); and Weale (*22*) has reported finding this region of his own eye markedly blue-sensitive relative to the fovea and parafovea.

Spectral sensitivity at the level of the cones. The data for R.H. can therefore be brought to the cone level by adding to her spectral sensitivities the average ocular and macular absorbances shown in Fig. 5; and the data for D.G. can be similarly corrected by adding her own denser ocular and macular absorbances to her spectral sensitivity curves. In this way the curves shown in Fig. 6 are obtained. Below 400 mμ, where these corrections are unreliable, the curves are drawn with broken lines.

The sensitivity curve of the dark-adapted fovea at the cone level consists of a major band showing a peak at about 550 mμ in both observers,

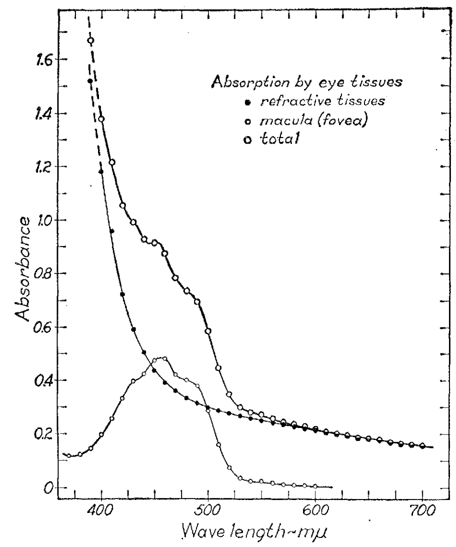


Fig. 5. An estimate of the average absorption by the dioptric tissues of the human eye (cornea to retina) and of the macular pigmentation (average of eight eyes) (*9*, and unpublished observations).

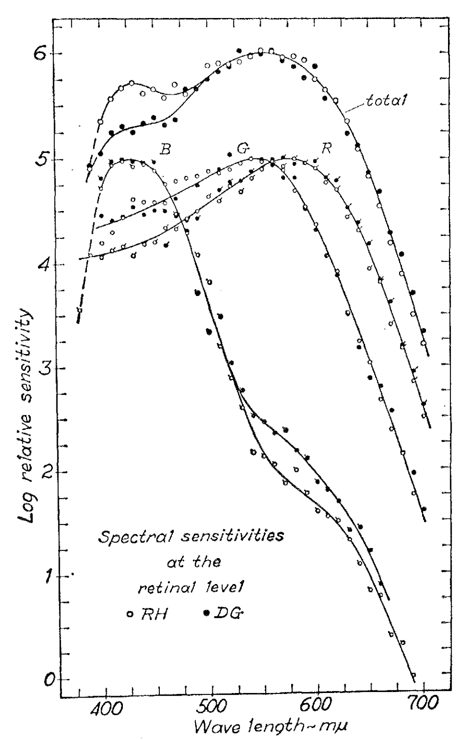


Fig. 6. Spectral sensitivities of R.H. and D.G., as in Figs. 2 and 3, corrected for ocular and macular absorptions. The resulting curves are as though measured at the level of the cones, and have the force of action spectra or absorption spectra of the foveal visual pigments. The sensitivity of the dark-adapted fovea ("total") displays a main peak at about 550 mμ, and a minor peak or inflection at about 430 mμ due to the blue-receptor, in which R.H. is particularly rich. The action spectra of the blue-, green- and red-sensitive pigments, following individual correction for ocular and macular absorptions, are invariant in shape and position, with λ_{max} at about 430, 540, and 575 mμ.

with a minor maximum or inflection in the blue. In the "corneal" curves of Figs. 2 and 3 the inflection in the blue was caused mainly by the depression of sensitivity in this region by the macular pigmentation. Now this factor has been removed, and the remaining bulge of sensitivity in the blue is caused by the blue-receptor. R.H., who is particularly rich in blue-sensitive cones or pigment, displays a maximum at about 430 mμ; but even the curve for D.G., which represents the average condition more closely, has a broad inflection in this region.

The curves for the individual receptors in Fig. 6, to the degree that the corrections are adequate, should represent the intrinsic action spectra of the blue-, green-, and red-sensitive pigments, and by the same token their absorption spectra—in terms of log relative absorbance—as measured *in situ*. They have many interesting features: (i) The maxima now lie at about 430, 540, and 575 mμ. (ii) Though the "corneal" sensitivity curves of these two subjects differ in shape and position, the corrected curves for blue (*B*), green (*G*), and red (*R*) are invariant, as they should be if they represent the action spectra of single pigments. A small difference appears only at long wavelengths in the *B* curve, one indication that the broad inflection in this region is due to the residual sensitivity of the other receptors rather than to the blue-receptor itself. (iii) These curves, unlike those for the "corneal" sensitivities, remain high at short wavelengths. The absorption spectra of all known visual pigments remain at least 1/5 as high in the violet and near ultraviolet as at their peaks (*23*). In Fig. 6 the *G* and *R* curves fall at 400 mμ to 22 and 14 percent of their maxima, not a bad approximation to the behavior of absorption spectra in view of the uncertainties of correction for ocular transmission at short wavelengths. The *B* curve at 400 mμ is about 0.6 of its maximum.

Figure 7 shows the same data plotted on the more familiar arithmetic ordinates. The features just described appear more clearly here. The same figure shows with broken lines the difference spectra of the green- and red-sensitive pigments of the human fovea, measured *in situ* by Brown and Wald (*9*). The difference spectrum of the green-sensitive pigment agrees well with the present measurements, except for the expected falling off of the difference spectrum below about 510 mμ owing to the formation of colored products of bleaching (retinaldehyde). The difference spectrum of the red-sensitive pigment, however, lies at slightly shorter wavelengths (λ_{max} 565 to 570 mμ) and is somewhat broader than the action spectrum. Both types of departure suggest that in measuring this difference spectrum, some green-sensitive pigment had been bleached

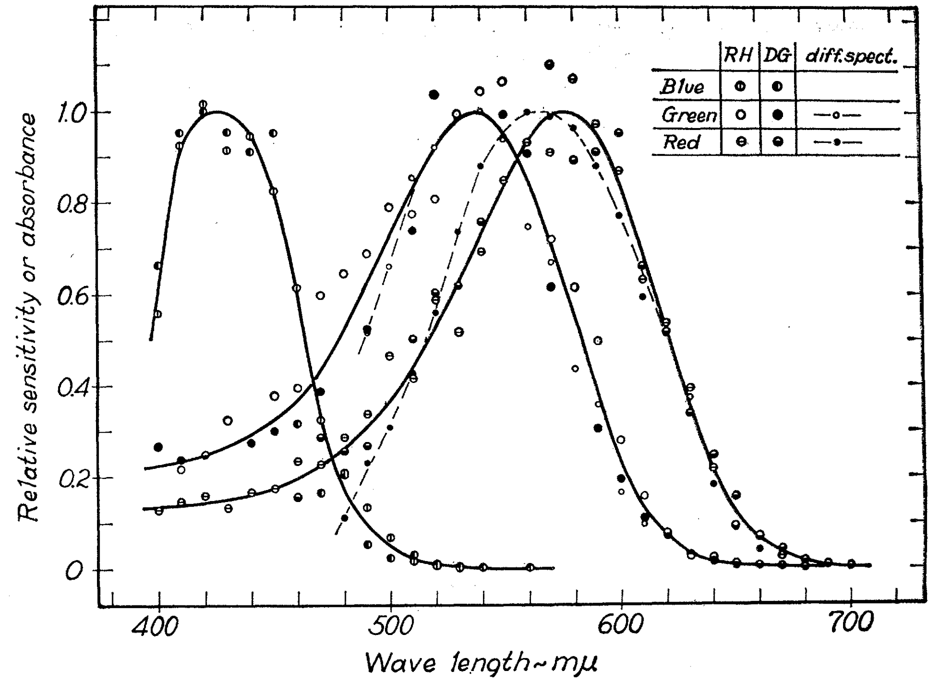


Fig. 7. Action spectra of the color-vision pigments of R.H. and D.G., corrected for distortions caused by ocular and macular absorptions. λ_{max} of the blue-, green- and red-sensitive pigments appear at about 430, 540, and 575 mμ. Difference spectra of the green- and red-sensitive pigments measured directly in the human fovea (*9*) are shown with broken lines. All curves have been given the same arbitrary height for comparison.

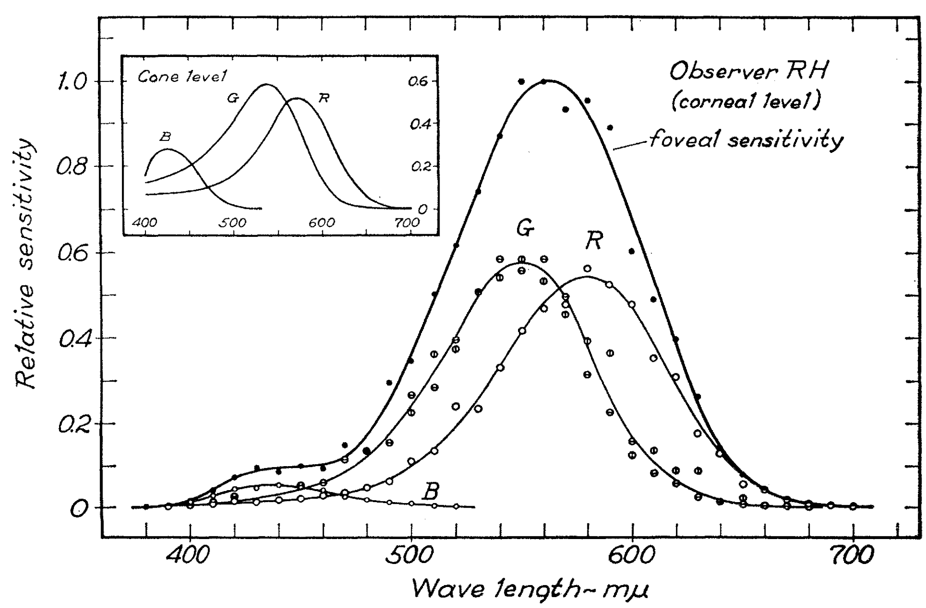


Fig. 8. Contributions of the individual color-receptor mechanisms to the total foveal sensitivity of R.H. The main graph shows measurements at the corneal level, the inset, corresponding curves at the level of the cones. In this particularly blue-sensitive observer, when the total foveal sensitivity is given a maximal height of 1.0, the heights of the *B*, *G*, and *R* curves are as 0.053 : 0.575 : 0.542 at the corneal level, and 0.28 : 0.59 : 0.52 at the level of the cones. In the average observer the blue-component is only about one-third as high.

along with the red-sensitive pigment. The present measurements not only represent absorption rather than difference spectra, but seem to involve a more complete isolation of the red-sensitive pigment than we had achieved previously.

Discussion

Composition of total foveal sensitivity. Figure 8 assesses the contributions of the three receptor pigments to R.H.'s total foveal sensitivity, as measured at the corneal level (main graph) and that of the cones (inset). R.H. was chosen for this computation because of her blue-richness, ensuring that her blue-receptor would appear significantly, as it might not in an average observer.

The computation starts with the recognition that beyond about 650 mμ the red-receptor accounts entirely for the total sensitivity. One can infer this not only from the curves of Fig. 7, but from the fact that beyond this wavelength hues are no longer discriminated—every wavelength matches every other in hue, an expression of the fact that only one type of receptor still functions.

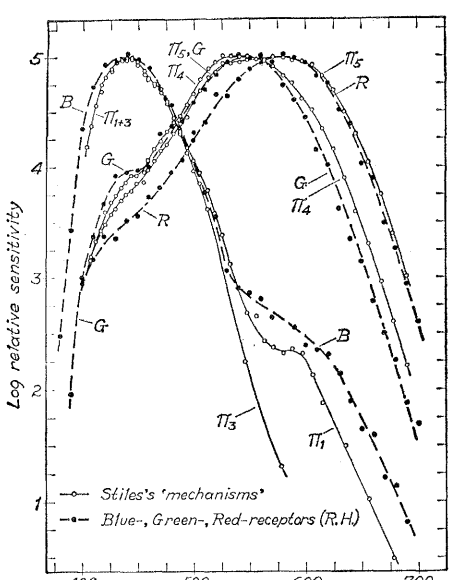


Fig. 9. Spectral sensitivities of R.H.'s foveal pigments (B, G, R) compared with Stiles's color-vision "mechanisms." These curves are uncorrected for ocular and macular absorptions, and have all been brought to the same arbitrary height for comparison. Stiles's blue-mechanisms π_1 and π_3 agree in the main with B, though displaying less long-wavelength shoulder, which is apparently extraneous. Stiles's green-mechanism π_4 is broader than G, implying a less complete isolation of the green-sensitive pigment. Stiles's red-mechanism π_5 follows almost exactly the envelope of the G and R curves, and apparently involves both pigments.

I begin therefore by fitting the red-receptor curve to the total sensitivity curve at long wavelengths, using such a logarithmic plot as Fig. 2, which offers a long stretch of these curves for matching between 650μ and 700 mμ. This sets the height of the red-receptor curve in the composite function. Then, subtracting the red-sensitivity data from the total, in such an arithmetic plot as Fig. 8, yields the vertically barred circles (plotted only to 500 mμ, below which the blue-sensitivity function would intrude). R.H.'s directly measured green-sensitivity data, brought to the same height, are shown in Fig. 8 with horizontally barred circles. The good agreement of both sets of points speaks well for the accuracy of the analysis. Subtracting the sum of the red- and green-sensitivity curves from the total indicates the height of the blue-sensitive component; and R.H.'s blue-sensitivity data, brought to this height, are shown in Fig. 8 as small open circles. The ratios of sensitivity maxima in this subject come out to be $R:G:B = 0.54 : 0.575 : 0.053$.

The ocular and macular absorptions particularly depress the sensitivity of the blue-receptor. A comparable analysis of spectral sensitivity at the level of the cones is shown in the inset of Fig. 8. The ratios of maxima are now $R : G : B = 0.52 : 0.59 : 0.28$, that is, about $1 : 1.13 : 0.54$.

It has already been stressed that R.H. is particularly blue-sensitive. The same analysis carried out with her red- and green-sensitivity curves and the average photopic luminosity function leaves no room at all for a blue-receptor; the sum of the red- and green-sensitivities accounts for the total within the errors of measurement. Other data, however, indicate that in the average observer the blue-sensitive component is about 1/3 as high as in R.H. In the average normal observer, therefore, when the total luminosity curve is set at a maximum of 1.0, the component curves should have maxima $R : G : B$ of about $0.54 : 0.58 : 0.018$ at the corneal level [compare Pitt (*24*), $0.50 : 0.58 : 0.015$]; and $0.52 : 0.59 : 0.09$ at the level of the cones.

Segregation of visual pigments in cones. Though the method of selective adaptation tends to isolate visual pigments rather than types of cone, for cones that contain only one pigment it does both.

The yellow lights used to isolate the spectral sensitivity of the blue-receptor cause so little light adaptation in the violet region (Figs. 2–4) that it seems unlikely that the blue-sensitive cones contain appreciable amounts of other visual pigments. It is known that bleaching very little visual pigment causes a large rise of threshold (*25*); and if the blue-sensitive cones contained considerable green- or red-sensitive pigment, the bleaching of the latter should raise their thresholds much higher than we observe in isolating the blue-sensitive pigment.

A like inference can be drawn from the fact that hue discrimination ceases beyond about 650 mμ, owing apparently to the fact that only red-sensitive cones continue to function. If the blue- and green-sensitive cones contained red-sensitive pigment, they should still function at such long wavelengths, and it should still be possible to discriminate between hues. It is probable, therefore, that neither the blue- nor the green-sensitive cones contain red-sensitive pigment.

These arguments leave open the possibility that the red-sensitive cones contain mixtures of visual pigments.

Blue or violet as a primary sensation. This distinction, though irrelevant to the main burden of this paper, has plagued color vision theory since its beginnings. After careful consideration, Young, Helmholtz, and König all settled upon violet rather than blue as the primary color sensation. In an earlier investigation I chose the same course (*12*, *21*). It is not common practise at present, however, and I depart from it here only to avoid raising an extraneous issue.

Comparisons with other measurements. The comparison of Stiles's measurements (p. 1016 of this issue), in which he used much the same techniques of selective adaptation as in the present work, with mine shows that his curve I (λ_{max} 443 mμ) is almost identical with the peak of my curve for the blue-receptor. His curve M comes closest to my green-receptor curve, though skewed toward shorter wavelengths, with λ_{max} about 533 mμ. Stiles's curve H, the closest to mine for the red-receptor, displays a peak near 590 mμ superimposed on a general rise of sensitivity toward shorter wavelengths. The divergences from my measurements in curves M and H seem to go with different choices of adapting lights and much lower intensities of adaptation. Other of Stiles's curves display two, in some instances (*G* for example), even three maxima from the individual receptors (compare Fig. 4).

It is more informative to make such comparisons with Stiles's color "mechanisms," based upon his extensive measurements of increment thresholds on backgrounds of graded brightness (*8*). Such a comparison with my measurements on R.H.—chosen because they involve close to average ocular and macular absorptions—is shown in Fig. 9.

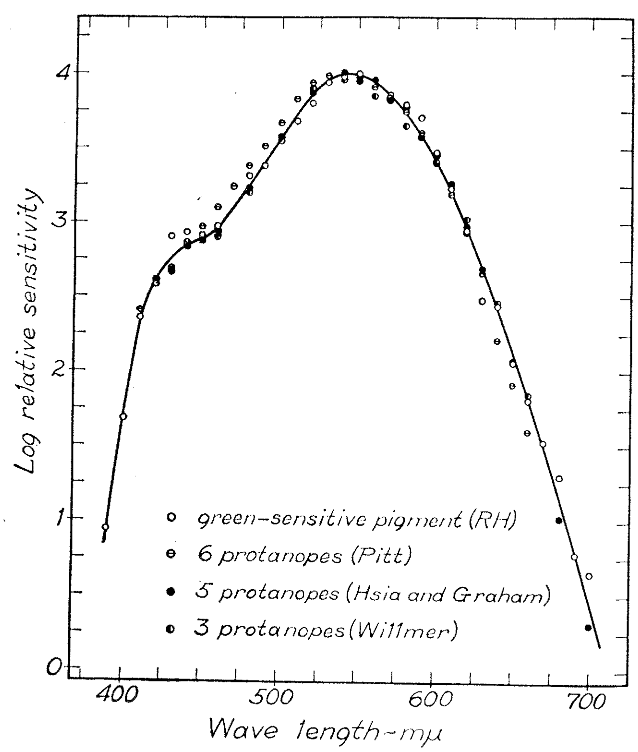
In evaluating his experiments, Stiles invoked two criteria: homogeneity of the relation connecting increment threshold with brightness of background, and conformity with what he calls "displacement rules"—that is, invariance of shape of the sensitivity function with the conditions of adaptation. These seem to me to imply two different approaches to the underlying mechanisms, the first physiological, the second photochemical. Homogeneity of the increment threshold function probably distinguishes a single neural unit, involving one or more cones and their central connections; whereas conformity with the "displacement rules" indicates the isolation of the action spectrum of one visual pigment. Among Stiles's "mechanisms," only those associated with the blue-receptor (π_1, π_3) obey the displacement rules. The green-mechanism (π_4) and the red-mechanism (π_5) do not, and must therefore involve mixtures of visual pigments.

The comparison shown in Fig. 9 reveals a number of interesting features. In π_1 and even more in π_3, Stiles has achieved more complete isolations of the blue-sensitive pigment than mine. π_3 indeed displays a single-banded action spectrum, with no indication of a shoulder at long wavelengths. This series of curves, added to what has gone before, makes it relatively certain that the long wavelength shoulder is not an intrinsic part of the action spectrum of the blue-sensitive pigment.

My measurements of the green-receptor display a narrower band than Stiles's π_4, implying a more complete isolation of the action spectrum of the pigment. This is implied also in the failure of π_4 to follow the displacement rules. (My measurements also display a slightly higher shoulder in the blue, owing probably to individual differences in macular pigmentation.)

The most illuminating comparison, however, involves Stiles's π_5, for as Fig. 9 shows, this traces almost perfectly the envelope of my curves for the green- and red-sensitive pigments. I think there can be little doubt that the π_5 mechanism depends upon roughly equal contributions from both pigments. The interesting question is whether such a mixture of pigments is present in the red-sensitive cones or in some other way converges its effects upon a single neural channel—that is, whether π_5, though composite in terms of pigments, may represent a single physiological mechanism. It may be recalled that my discussion of the segregation of visual pigments among the cones left this possibility open in the case of the red-receptor.

It is consistent with this interpretation that the red- and green-receptors seem to follow a different principle in combining to form the π_5 mechanism than in composing the luminosity curve. In the latter instance they simply add together, as in Fig. 8, a straightforward photochemical type of behav-



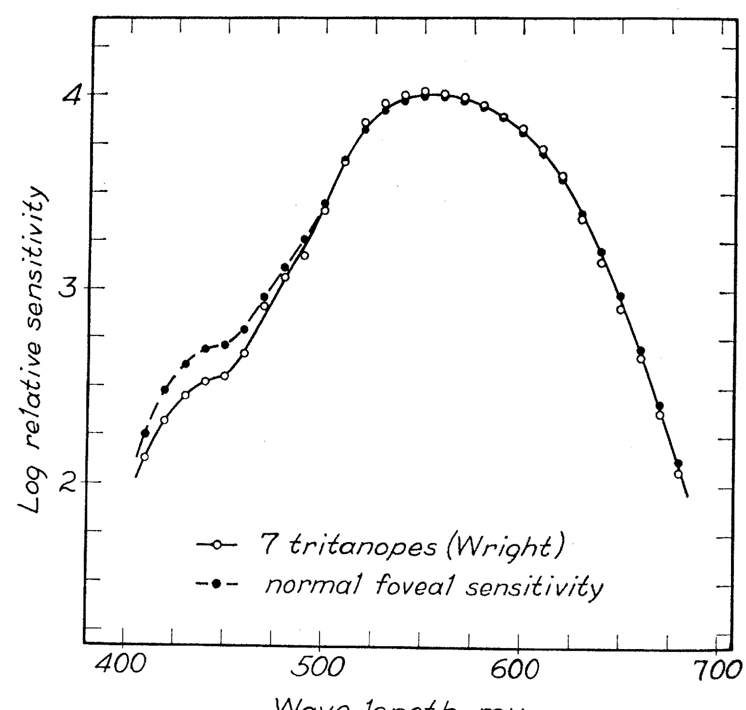


Fig. 10 (left). Action spectrum of R.H.'s green-sensitive pigment, measured at the corneal level, compared with the foveal luminosity function of 14 protanopes. These dichromats apparently possess only the green- and blue-sensitive pigments, the latter contributing so little to the luminosity function as hardly to appear in the measurements. It can be concluded that protanopes lack the red-sensitive pigment, and in this sense are literally red-blind. Fig. 11 (right). The average photopic luminosity function of 7 tritanopes measured by Wright (*42*), compared with that of normal observers. The small loss of sensitivity of tritanopes in the blue and violet has the shape and position of the action spectrum of the blue-sensitive pigment, with λ_{max} about 450 mμ, and a difference at that wavelength of about 0.23 log unit, representing a loss of relative sensitivity of about 40 percent. Such observers appear to lack the blue-sensitive pigment, and in that sense are blue-blind.

ior. In making up π_5 however, the increment threshold at each wavelength seems to depend primarily on whichever receptor is the more sensitive, so yielding a peculiarly broad function—considerably broader than the total luminosity curve—that represents the *envelope* of the red- and green-sensitivity curves rather than their sum.

Rushton (*26*) and Weale (*27*) have attempted the superbly difficult feat of measuring the difference spectra of foveal pigments directly, by the spectrophotometry of light reflected from the fundus of the living eye after passing twice through the retina. Rushton originally reported finding green- and red-sensitive pigments at about 540 mμ and 590 mμ, Weale at about 540 mμ and 600 mμ. For understandable reasons this procedure offered no approach to the blue-sensitive pigment; it has tended also to yield inconsistent results with the red-sensitive pigment. Rushton has recently "disclaimed" all his measurements of this kind prior to 1963 (*28*). We are left with (i) his new measurements of the green-sensitive pigment which, though they rise from the red to a maximum near 550 mμ, do not descend again significantly, that is, do not describe a peak (*29*); (ii) a computation "correcting" the absorbance of this pigment from a measured value of 0.07 to 0.35 (*30*), which I judge to be at least 5 and perhaps as much as 10 times too high (*9*); and (iii) a remeasurement of the red-sensitive pigment in deuteranopic (*31*) and normal (*32*) eyes, which, though accompanied by elaborate tests to show that a single pigment was measured, is said to match Stile's π_5 mechanism, which we have just seen to involve both the green- and red-sensitive pigments.

This procedure has yielded valuable information on the rise and fall of visual pigments in the living eye, and seems to measure reasonably well the difference spectrum of such a relatively dense pigment as rhodopsin; but it may not be capable of measuring reliably the difference spectra of the foveal pigments.

Color-Blindness

"The mathematical expression of the difference between Colour-Blind and ordinary vision is that colour to the former is a function of two independent variables, but to an ordinary eye, of three; and that the relation of the two kinds of vision is not arbitrary, but indicates the absence of a determinate sensation, depending perhaps upon some undiscovered structure or organic arrangement, which forms one-third of the apparatus by which we receive sensations of colour."

—JAMES CLERK MAXWELL
letter to G. Wilson, 1855

Whereas normal human color vision is trivariant, the usual types of color-blind vision are divariant (*33*). Young suggested that the red-blindness of his contemporary, the chemist Dalton, might be caused by the lack of one of the three color mechanisms (*1a*). This idea, taken up by Helmholtz and Maxwell as a general explanation of color-blindness, later ran into the difficulty that many color-blind persons possess a nearly normal spectral sensitivity (*34*, *35*). Fick (*36*) suggested that in such dichromats, two of the color channels—red and green—may be fused to yield a single sensation. Yet there has been no common agreement on this or other mechanisms of color blindness, and some years ago it became customary to bypass questions of mechanism by using arbitrarily—though he himself attached mechanisms to these terms—von Kries's classification of dichromats into protanopes, deuteranopes and tritanopes (*37*).

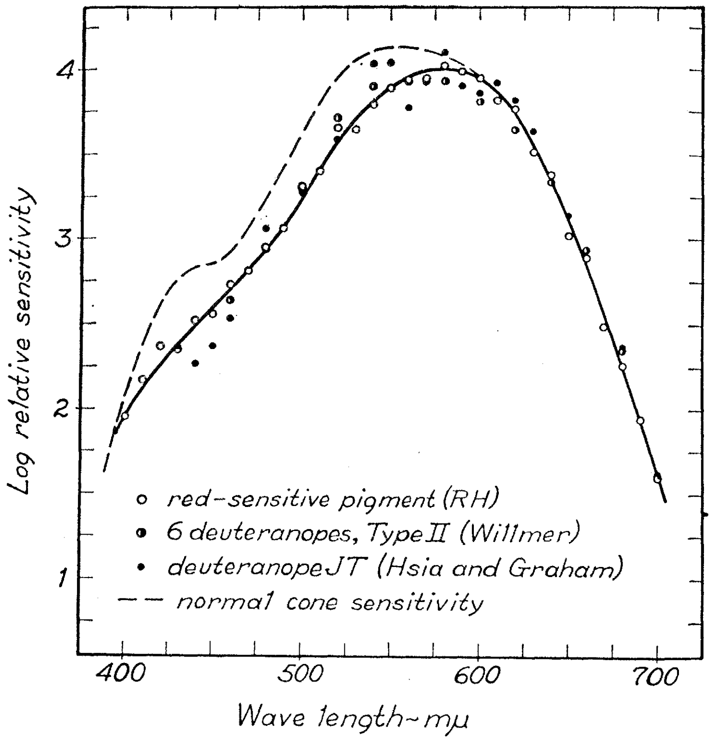
Most color-blind persons—about 2 percent of all human males—are protanopes and deuteranopes. Both groups see only two hues in the spectrum, apparently blue and yellow (*38*; Graham, *6*), with a neutral point between that can be matched with white. The neutral points lie near 493 mμ in protanopes and near 497 mμ in deuteranopes, depending in part on the white chosen for matching (*34*). Protanopes and deuteranopes are therefore much alike except in one respect: the protanopes are abnormally insensitive to red light, whereas the deuteranopes are said to have a nearly normal spectral sensitivity. Tritanopes are rare (about 0.002 percent of men); they have an almost normal spectral sensitivity, and a neutral point at about 572 mμ.

One of the main difficulties in understanding color blindness is resolved with the recognition that it includes, not three, but four main types, and indeed two quite different kinds of "deuteranope." One of them lacks the green-sensitive pigment, and in this sense is literally green-blind; the other has all three foveal pigments in normal proportions, but the red- and green-mechanisms are coupled to form a single sensory system. This distinction, drawn clearly by Willmer, who called these deuteranopes of Types II and I (*39*), is fundamental to an understanding of the subject.

Figure 10 shows the foveal luminosity data of 14 protanopes measured by various observers, compared with the "corneal" action spectrum of R.H.'s green-sensitive pigment. The agreement of these data shows that, as usually supposed, protanopes lack the red-sensitive pigment. They possess also, like normal trichromats, so little blue-sensitivity that the total luminosity function is dominated by the green-sensitive pigment alone. [The data for R.H. are chosen for these comparisons because she possesses close to the average ocular and macular transmissions. The measurements of Pitt (*40*) involved comparisons between the halves of a 2° unfixated field, those of Hsia and Graham (*14*) a centrally fixated 42′ field, and those of Willmer (*39*) a 10′ field such as he believed to be blue-blind even in trichromatic subjects (*41*).]

A word should be said here about neutral points. Though for a variety of reasons they may depart considerably from the wavelengths at which the sensitivity curves of dichromats cross in such a diagram as Fig. 8, they do bear a relationship to such crossing-points. The fact that in protanopes a neutral point occurs near 493 mμ suggests a crossing of the *B* and *G* curves near that wavelength. Obviously in Fig. 8 this crossing comes too low, near 450 mμ, even though drawn for R.H., for whom the *B* curve is about 3 times as high as the average. Evidently the blue-receptor has a far larger white-making valence than its contribution to the foveal sensitivity function indicates; but that is another problem. Much the same comments will apply to the "deuteranopes" of Figs. 12 and 13.

Figure 11 shows the average foveal luminosity function of 7 tritanopes measured by Wright (*42*), compared with that of normal observers. The tritanope curve displays a small loss of sensitivity in the blue and violet. The difference between the normal and tritanope sensitivities has the same shape and position as the action spectrum of the blue-sensitive pigment. The loss of sensitivity is greatest at about 450 mμ, and is there 0.23 log unit (about 40 percent), about what is expected from the contribution of the blue-receptor to the spectral sensitivity



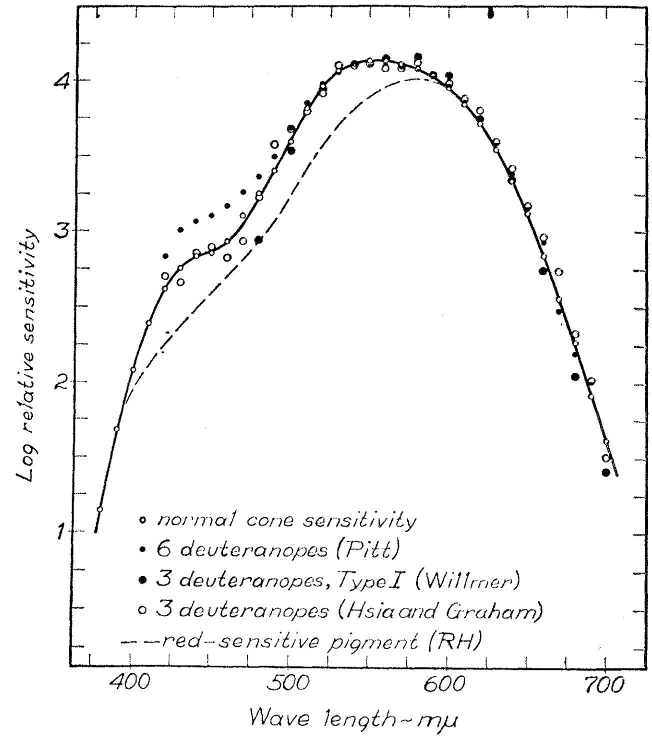


Fig. 12 (left). The foveal luminosity function of "deuteranopes" who display a relative loss of sensitivity at short wavelengths, compared with the action spectrum of R.H.'s red-sensitive pigment, measured at the corneal level. The good agreement of these data shows that this class of deuteranope lacks the green-sensitive pigment, and in this sense is literally green-blind. For comparison the normal photopic luminosity function is shown with a broken line. Fig. 13 (right). The foveal luminosity function of "deuteranopes" in whom this function is nearly normal, compared with that of trichromatic observers. For contrast with Fig. 12, the action spectrum of R.H.'s red-sensitive pigment is also shown with a broken line. This class of deuteranope possesses all three color-vision pigments in average proportions, but the red- and green-mechanisms are fused or confused so as to yield a single sensation. The high sensitivity in the blue in Pitt's measurements is probably due to his use of a relatively large and unfixated test field, extending beyond the central fovea.

of the normal observer. The presence of a neutral point in tritanopes at about 572 mμ is consistent with the crossing of the *G* and *R* curves near that wavelength (Fig. 8).

Figure 12 shows measurements on 7 "deuteranopes" whose spectral sensitivity curves correspond with the action spectrum of R.H.'s red-sensitive pigment. By the same token they depart widely from the average photopic luminosity function, shown here with a broken line. Such subjects apparently lack the green-sensitive pigment.

There are therefore three types of dichromat, each of which lacks one of the color-vision pigments. They might in that sense be called red-, blue- and green-blinds or, if Greek roots are preferred, anerythropes, acyanopes and achloropes. The general phenomenon might be called *achromia.*

What central arrangements one postulates to accompany the presence of only two visual pigments in such dichromats depends upon how seriously one takes the reports that protanopes and deuteranopes see the long-wavelength end of the spectrum as *yellow.* I am inclined to think them significant, particularly in view of the observations on unilateral dichromats, who match all wavelengths longer than the neutral point in the dichromatic eye with yellow in the normal eye (*38, 43*). On this basis the simplest assumption is that such dichromats retain all three sensory channels and the capacity to experience all three primary sensations, but that in each case two sensations are excited by a single visual pigment. So one might assume that in protanopes the green-sensitive pigment, and in the deuteranopes of Fig. 12 the red-sensitive pigment, excites indiscriminately the red- and green-sensations, thus yielding a sensation of yellow.

Another type of color blindness involves an altogether different mechanism. Here all three visual pigments are present, often in normal proportions, but evoke only two types of sensory response; that is, the effects of two of them converge so as to excite a single sensation.

What is probably the more prevalent type of "deuteranopia" is of this nature. Figure 13 shows that the luminosity function of this class of subject agrees with that of the average trichromat. (In this figure, I plotted Pitt's average for 6 "deuteranopes." The increased sensitivity to blue in these data may be due to Pitt's use of a 2° field which is unfixated and therefore extends somewhat beyond the central fovea.) If such subjects see wavelengths longer than the neutral point as yellow, they may possess not only all three visual pigments in normal proportions, but also all three sensory mechanisms. The essential disability would then involve only a confusion of the red- and green-pathways, such that both the red- and green-sensitive pigments, whether in separate cones or mixed in the same cones, excite both pathways indiscriminately and evoke the yellow sensation.

This type of color-blindness might be called a *synchromia*—in the present instance, red-green (*R-G*) synchromia. We can anticipate two further synchromias, red-blue (*R-B*) and green-blue (*G-B*). Either or both conditions may correspond with what has been described as tetartanopia, a form of dichromia in which the spectral sensitivity is normal, and *two* neutral points occur, at about 470 mμ and 580 mμ (*34*). It should be clear from Fig. 8 that a fused *B-G* mechanism would cross the *R* curve, or a fused *B-R* mechanism 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.

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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-

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