RODS, CONES, AND THE CHEMICAL BASIS OF VISION

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I. In the last few years there has accumulated a considerable amount of new and highly precise data describing various visual functions. In addition, many of the older measurements have been freshly evaluated, and the whole field of vision has achieved a quantitative form not recognized a generation ago. The first purpose of the present paper is to bring together these recent measurements and evaluations, and to show how easily and strikingly they fall into the pattern of the Duplicity Theory which separates vertebrate vision into cone function and rod function.

The value of the material is by no means exhausted by this treatment. Rather, it is enhanced because of the identification of specific measurements with known morphological units, whose chemical properties may then be investigated. The second purpose of this summary is to deal with the quantitative aspects of the data as they bear on the possible chemical systems present in the retinal receptor elements.

II. DUPLICITY THEORY. The retinas of most vertebrates contain two different types of receptors,—cones and rods; and this fact has led to the notion that the vertebrate retina is not one sense organ, but two.

Consider the human eye. Structurally the center of the retina is occupied exclusively by cones, while the rest of the retina contains rods and cones, with rods increasingly predominant toward the periphery. Since at high illuminations vision is most efficient with the center of the retina, whereas at low illuminations it is most effective with the periphery, the idea of a double visual organ associates the cones with vision at high light intensities, and the rods with vision at low light intensities. Moreover, since we see color best at high intensities and see no color at low intensities, we may consider the cones as specific receptors for color, and the rods as the general receptors for light regardless of color.

In essentially this form the idea for a retinal double sense organ was proposed by Max Schultze in 1866 on the basis of the histological studies which he made of the vertebrate retina, coupled with the physiological

knowledge contributed by his contemporaries Aubert (1865) and Helmholtz (1866). However, no one seems to have paid any attention to the idea,—which is curious because Schultze was an important figure in his time, and his histological work was recognized and appreciated. The neglect of the concept was so complete that it is not even mentioned in the second edition of Helmholtz's *Physiological Optics*, which appeared in sections between 1884 and 1894, and was finally published as a whole in 1896. By that time the notion of a double retinal function had been independently suggested by Parinaud (1881) as the result of his observations on night-blindness and other pathological disturbances of vision, and by von Kries (1895) as an explanation of the many properties and ramifications of the Purkinje phenomenon (Purkinje, 1825; Dove, 1852).

The observations of Purkinje and later of Dove had shown that when widely different colors are matched in brightness at high intensities, the matches are not valid at low intensities, and the reverse. Parinaud (1884, 1898) had tried to explain the presence of this phenomenon in the visual periphery, as well as its absence in the fovea, in terms of visual purple. But it was von Kries' merit to have attributed it correctly to the different sensibilities of the rods and cones in the spectrum,—a concept which is still basic.

Since its reintroduction by von Kries and Parinaud, the idea of a double retinal function has been called the Duplicity Theory, and has persisted to the present, though not without the criticisms of Hering (1915) and Hess (for a summary see Hess, 1920) made largely as the result of experiments which we know now to have been erroneous (*cf.* especially Dieter, 1924; and Gross, 1928). With the years, the evidence for it has become more extensive and impressive; and when before his death von Kries (1929) summarized its status, he could feel certain that the double function of the retina in terms of rods and cones was a well-established concept in physiology.

The summary which von Kries wrote rests in the main on the roughly quantitative implications of the Purkinje phenomenon. To a certain extent von Kries was unaware of the later developments in vision, and did not include them in his treatment. But even since 1929 the newer data which have become available are not only more plentiful than those known to von Kries, but possess a much higher precision and definitiveness. For them also the Duplicity idea serves as a simple reference frame.

III. SPECTRAL SENSIBILITY. a. *Low intensity and rods.* The oldest

physiological difference recognized between rods and cones depends on the relative sensibility of the eye to the spectrum at low and at high intensities.   We shall consider this first as it relates to the rods.   When the visible spectrum is reduced to an intensity near the threshold and is viewed by a dark-adapted eye, it appears colorless.   Beginning perhaps with Ebert (1888) and Langley (1888), a number of investigators (Hillebrand, 1889; Koenig and Ritter, 1891; Abney and Festing, 1893; von Kries and Nagel, 1896; Schaternikoff, 1902; Pflüger, 1902; and Trendelenburg, 1904) studied the relation between wavelength and the amount of light required to produce a specific brightness at or near the threshold.

The main difficulty with this early work was that the energy distribution in the spectrum was not known, and therefore the relative effectiveness of the spectrum was dependent on the particular source of light used.   The best of the measurements were by Koenig, who corrected his data for spectral energy distribution in terms of Langley's measurements of sunlight.   Koenig found that no matter what the other visual characteristics of his various subjects were, their maximum visibility at low brightnesses was at about 500 mμ.

Thirty years after Koenig, Williams and I (Hecht and Williams, 1922) reinvestigated the relation with modern methods making our own energy measurements, and using 48 normal individuals in order to get an average function.   Later Kohlrausch (1923), Laurens (1924), and Sloan (1928) repeated the measurements with one observer each, and agreed with us in placing the maximum effectiveness of the low intensity spectrum at very nearly 510 mμ.   Our average data are shown in the lower portion of figure 1.   They give the relative energy required at the different wavelengths for the eye to see a light slightly above the threshold after an hour of dark adaptation.   There can be little doubt that these data represent a function of the rods.   At such low intensities the fovea, containing a predominance of cones, is completely blind; and the measurements are best made with large fields falling well in the periphery of the retina.

The effectiveness of the spectrum at low intensities has just been determined for two other mammals.   Graham and Riggs (1935) measured it with the white rat, using the retinal potential as an index; and Brown (1936) has examined it for the rabbit, using a conditioned respiratory reflex.   In both cases the spectral effectiveness is almost identical with what Williams and I found for the human eye.   The white rat's spectral sensibility is the same at high and low intensities; its vision is thus

entirely a rod function. This corresponds to the histological demonstration that its retina contains only rods and no cones, as well as no central region of compactly grouped elements (see especially Lashley, 1932).

It is obvious that human eyes which lack color vision completely, and therefore possess no cone function, should resemble the white rat's
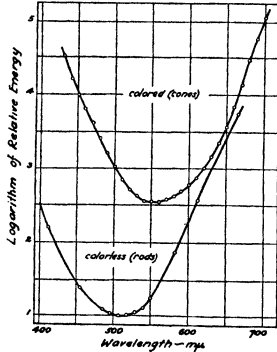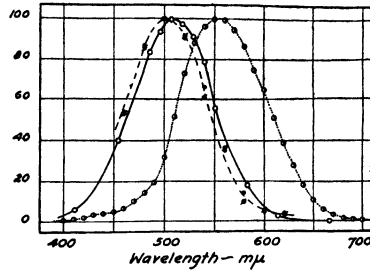

Fig. 1   Fig. 2

Fig. 1. Relation between wavelength and relative energy required to produce a specific visual effect at high and at low illuminations. The lower data are from Hecht and Williams (1922) and represent the relative energy required to produce a barely perceptible brightness after prolonged dark adaptation. The upper data are from Hyde, Forsythe and Cady (1918) and give the relative energy to produce a given high brightness, using only the fovea. The two curves are each accurately drawn from their separate data. Their vertical separation, however, has been arbitrarily arranged so that they are nearly coincident at the red end of the spectrum; this is a graphic expression of the fact that the colorless and color thresholds of the eye are nearly identical in the red.

Fig. 2. Visibility curves and the absorption spectrum of visual purple. The empty circles and continuous line record the relative effectiveness of the spectrum at the lowest intensities; they are the reciprocals of the energies in figure 1 so arranged that the maximum effectiveness is 100. The filled circles and those with a line through them are the absorption coefficients of visual purple of the rabbit and monkey respectively also computed for a maximum of 100; the measurements are from Koettgen and Abelsdorff (1896). The half filled circles and dotted line are the average data of Gibson and Tyndall (1923) for the visibility of the spectrum at high intensities by persons of completely normal color vision.

eye in this respect and should show the low intensity spectral effectiveness at all intensities. Measurements with a complete colorblind were first made by Donders (1882) and soon after by Koenig and Dieterici (1886). After Hillebrand's (1889) measurements at low intensities, it was apparent that the colorblind data, though secured at ordinary intensities, resembled the normal low intensity data secured with a simi-

lar spectrum. This was confirmed by Hering (1891), by Koenig and
Ritter (1891), later by May (1907) among others, and most recently
by Geldard (1933). Geldard was the first actually to determine the
energy distribution in the spectrum used for measurements with a
complete colorblind, and he found that even though the spectral sensi-
bility measurements were made at moderately bright intensities, the
resulting distribution practically duplicated our 1922 measurements
at threshold intensities shown in figure 1.

b. *Visual purple.* The most interesting property of the lower curve
in figure 1 is its relation to the absorption spectrum of visual purple,
the photosensitive pigment in the outer segments of the rods. Visual
purple was discovered by Boll (1876) and extracted from the retina by
Kuehne (1879) who determined many of its properties. Since then it
has been investigated by Koenig (1894), by Koettgen and Abelsdorff
(1896), and by Trendelenburg (1904, 1911), who were all mainly con-
cerned with its absorption spectrum; by Garten (1906, 1907) and by
Hosoya and Bayerl (1933) and by Hosoya (1933), who dealt with the
changes in the absorption spectrum during and after bleaching; by
Hecht and Chase (1934) and by Chase (1936), who have partially cleared
up the conflicting reports in the work of previous investigators; by my-
self (Hecht, 1920a, b; 1924b), and by Weigert and Nakashima (1929,
1930), who studied certain aspects of its photochemistry; and by Wald
(1933; 1934; 1935a; b; 1936), who has given important information about
its chemical constitution.

If visual purple is the photosensitive material responsible for rod
vision, then its absorption spectrum should be intimately related to the
spectral sensibility of the eye at low intensities. To make the compari-
son, it has to be assumed that a just perceptible visual effect requires
the absorption of a constant amount of energy, I_a, regardless of wave-
length. Strictly, the assumption should be that a constant number of
quanta is required, but because of the small range of wavelengths the
difference between the two is negligible. If I is the incident energy, a
the concentration of visual purple, and ϵ the absorption coefficient, then

$$I_a = I \, (1 - e^{-\epsilon a}) \tag{1}$$

in terms of Beer's law. The exponential expands into the series

$$e^{-\epsilon a} = 1 - \epsilon a + \frac{\epsilon^2 a^2}{1 \cdot 2} \cdots \tag{2}$$

in which terms having powers higher than unity may be neglected be-

cause only threshold effects and small concentrations are involved. Substituting in (1) and rearranging, we get

$$\epsilon = I_a/I\ a \qquad\qquad (3)$$

which puts the absorption coefficient as inversely proportional to the incident energy required for a threshold effect.

Koenig (1894) first made this comparison. His visibility data, corrected approximately for energy distribution in the spectrum, resemble the absorption data of visual purple secured from a single human eye, though the two maxima seem to differ by about 5 mμ. Later, Trendelenburg (1904, 1911) showed that the rate of bleaching of visual purple follows its absorption spectrum, and is closely related to the low intensity visibility curve as well. Trendelenburg made no measurements of spectral energy distribution; his results, approximately corrected for energy by Henri and Larguier des Bancels (1911), roughly resemble Koenig's findings.

An adequate comparison between the visibility curve and the absorption spectrum of visual purple was made possible only when the accurate data of figure 1 became available. Figure 2 shows this comparison between a, our data plotted as visibility, that is, the reciprocal of the required energy, and b, the absorption spectrum of monkey and of rabbit visual purple as measured by Koettgen and Abelsdorff (1896). The data of Koettgen and Abelsdorff are the most complete; however, because of the method used, their determinations at 440 and 420 mμ are probably in error, and have been omitted (*cf.* Garten, 1907; Chase, 1936).

Figure 2 shows that the two sets of data are almost identical but that the visibility curve is displaced about 7 mμ toward the red. This difference appears even in the older data of Koenig and of Trendelenburg. Since the low intensity visibility curves of the rabbit and of the white rat are practically identical with the one for man, this displacement relative to the absorption spectrum is present also for them. Moreover, the work of Chaffee and Hampson (1924) on the spectral sensibility of the frog's eye also shows a displacement of similar magnitude in relation to the absorption of frog visual purple as measured by Koettgen and Abelsdorff.

This displacement may be due to the difference in medium. Measured with a spectrophotometer, visual purple is in aqueous solution, whereas in the retina visual purple is in the dense and highly refractive outer segments of the rods. In terms of Kundt's rule (Kundt, 1878) the shift is in the right direction, that is, the absorption maximum moves

toward the red as the density and refractive index of the medium increase (*cf.* especially Becking and Koning, 1934). Therefore we may conclude that the dim visibility curves of the human eye, the rat eye, the rabbit eye, and the frog eye, correspond to the absorption spectrum of visual purple ·in the condition in which it is present in the terminal segments of the rods.

An additional bit of proof comes from the fact that fresh water fishes have a visual purple whose maximum is not at 500 mμ but at 540 mμ (Koettgen and Abelsdorff), though marine fishes seem to fall between these two values (Bayliss, Lythgoe, and Tansley, 1936). The visual purple of the sunfish *Lepomis* has its maximum absorption at 540 mμ, and Grundfest (1932a) has found that the maximum of its low intensity visibility curve also comes at nearly the same place.

c. *High intensities.* The visibility of the spectrum at high brightnesses is usually found by measuring the relative energy at different wavelengths required to match a high constant brightness. Such measurements date from Fraunhöfer (1814), who used the relative brightness in the spectrum as a substitute for the then unknown energy distribution. With the introduction of energy measurements by Langley, the visual effectiveness of the spectrum at high intensities has been repeatedly determined.

The best of the earlier measurements were made by Koenig and Ritter (1891) who compared by direct photometry different parts of the spectrum with one portion of it. This is a fairly brutal method; and since then, various tricks have been devised to avoid the subjective difficulties of such heterochromic comparisons. Measurements have been made with many observers by Hyde, Forsythe, and Cady (1918), by Nutting (1920), by Ives (1912b), and by Coblenz and Emerson (1918). Many other investigators, too numerous to record, measured the distribution for their own eyes, but in most cases, except those specifically mentioned, the energy distribution of the source was not known, and the data are useless as absolute statements of the relation between energy and wavelength.

Probably the most adequate data are by Gibson and Tyndall (1923), using heterochromic comparisons of small wavelength steps. The averages of some fifty color-normal individuals are in figure 2; the data are almost identical with the earlier measurements of Hyde, Forsythe and Cady, of Ives, and of Coblentz and Emerson. The maximum is at 555 mμ, which is 45 mμ farther toward the red than the low intensity visibility curve also shown in figure 2.

Anatomically, the high intensity measurements in figure 2 certainly

represent the behavior of cones, since the observations were made with small fields falling within the fovea which is composed mostly of cones. The brightness was quite high, with color vision dominating. However, even with low brightness and dark adaptation, cone behavior alone is apparent in visibility curves provided only small fields of about 1° are used (Sloan, 1928).

Precisely what the cone visibility curve represents is hard to say. Ultimately, of course, it must be the sum of the absorption spectra of the sensitive materials in the cones. At the present time it is generally supposed, in accordance with Young's (1807) idea of the basis for color vision, that there are three types of cones, each with its own sensitive substance. But there is no unanimity in the suggestions for the spectral sensibility distributions of the three receptors. Young supposed their absorption maxima to be widely different in the spectrum, and this supposition was adopted by Helmholtz (1866), by Koenig and Dieterici (1892), and has persisted up to the present (cf. Wright, 1934). Helmholtz later (1891) changed his mind and for very good reasons made the three absorption curves resemble one another; unfortunately his particular curves each have two maxima, and when added together do not even remotely resemble the visibility curve. I have shown (Hecht, 1930; 1931; 1932) that in order to describe with any precision the quantitative data of color vision, particularly those involving saturation, one must assume that the three cones possess absorption spectra which resemble one another closely rather than the reverse. Such absorption curves describe the data, and when added together reproduce the visibility curve exactly.

To settle the matter it would be well to isolate the cones, or to extract their sensitive materials, and to measure them. Unfortunately this has so far proved impossible. Even the evidence presented by von Studnitz (1932) to prove that the cone retina as a whole shows decreased absorption after exposure to light is rather dubious; photomechanical changes in such retinas are known to occur (Garten, 1907; Arey, 1915; Detwiler, 1916), and these would be sure to influence the transmission of a semi-opaque tissue like the retina.

d. *Other animals.* Other vertebrates which, like man, also possess both cones and rods can be expected to show two types of visibility curves, one at low intensities and another at high intensities. Such an expectation was first confirmed by Himstedt and Nagel (1900) and in greater detail by Piper (1904; 1905a) who found two spectral sensibility curves for the frog's eye by measuring the retinal currents produced on

illumination (cf. however, Chaffee and Hampson, 1924). Moreover Piper (1905a) found that day birds such as the domestic hen and the pigeon show only one spectral sensibility distribution which corresponds to the high-intensity cone visibility curve of man; while night birds like the owl, and mammals like the dog, cat, and rabbit also show only one sensibility curve corresponding in this instance to the rod visibility curve of man.

Fish are known to have rods and cones (Schultze, 1866; Wunder, 1925); and Bauer (1910, 1911) and von Frisch (1925) found that they show the Purkinje phenomenon, indicating that the high and low intensity visibility curves differ in position on the spectrum. Grundfest (1932b) actually determined the two curves for the sunfish Lepomis and found the low intensity maximum at 540 mμ and the high intensity maximum 30 to 60 mμ farther in the red. The average shift between the two maxima is about the same as for the human eye and for the frog eye (Himstedt and Nagel, 1900; cf. especially Kohlrausch, 1931a).

e. Consequences. At low intensities the visibility curve is determined by the rods because the cones do not function, while at high intensities it is given by the cones because of their numerical preponderance in the fovea (cf. Abney and Festing, 1891; Rosenberg, 1928). What will happen at intermediate intensities in retinal locations having rods and cones depends on whether the contributions from the two receptor systems remain separate or are fused in the resulting sensory effect.

With brightness the situation is simple. Koenig and Ritter (1891) were able to show for the human eye that the relative brightness of the spectrum at different intensities passes gradually from one system to the other, and that at some intermediate intensities the visibility of the spectrum actually shows two maxima (cf. also Sloan, 1928; Forbes, 1929). Clearly, brightness is a function in which the two retinal systems pool their effects additively.

There are other functions in which the two systems behave more independently, and in which the transition from one to the other is fairly sharp. In order to understand the behavior of such functions, it is well to consider the visibility curves again, but from a slightly different angle. The two curves are shown in figure 1 in the form of relative energy for a constant brightness against wavelength. Each curve is accurate by itself, but the vertical separation between the two is arbitrary because its exact extent varies somewhat with the position on the retina.

Beginning at the lowest energy level and moving vertically along any

ordinate, light produces its first visual effect when its magnitude reaches the rod curve. The particular function continues to be controlled by the rods as the energy increases, until the cone curve is reached. At this point if cone activity is independently recognized, a definite change in the character of the function should become apparent, which will be maintained as the intensity increases. The significant feature of figure 1 is that because of the different minima of the curves, this rod-cone interval must vary with the wavelength, being very small in the red, and large in the blue.

A case in point is the sensation of color, characteristic of cone function. The intensity range between rod threshold and cone threshold in figure 1 is controlled by rod function and appears colorless. Above the cone curve, color makes its appearance. The rod-cone, or colorless-to-color, interval should then be small in the red and large in the blue. This is indeed the fact, as shown by the work of Charpentier (1880) and Parinaud (1898) who refer to the difference between rod and cone thresholds as the photochromatic interval.

In respect to intensity and spectrum, all the visual phenomena to be described show a sufficient degree of independence in rod and cone function for their effects to be easily differentiated and understood in terms of figure 1.

IV. DARK ADAPTATION. a. *Rods and cones.* The capacity of the human eye to increase in sensibility during a stay in the dark was first described by Aubert (1865). Since then, this phenomenon has been frequently investigated in man and other animals (for summaries see Adams, 1929; Müller, 1932; and Hecht, 1934a). For the human eye, the data fall quite neatly into what may be expected in terms of rod and cone function.

The earliest measurements were by Piper (1903) and were confirmed by Nagel (1911) and by others since. The determinations were made with white light, large measuring fields, and peripheral observation. In general, the measurements show a continuous decrease in threshold extending for about 30 minutes and covering an intensity range of about 5000 to 1 units of intensity.

This change was correctly ascribed to the rods because of its location in the retinal periphery and because of the lack of color at the threshold. In fact, it became generally accepted that the rods alone could dark adapt while the cones could not, though there was some evidence (Nagel and Schaefer, 1904; Inouye and Oinuma, 1911; Dittler and Koike, 1912) to show that the cones do adapt slightly.

The matter was finally settled when the dark adaptation of the rod-free area of the fovea was accurately measured (Hecht, 1921), and the reasons for the previous failures became apparent. These measurements were confirmed next year by Kohlrausch (1922) and later by Graham (1930). Figure 3 shows the data, from which it is apparent that foveal dark adaptation is very rapid and practically over in 3 minutes. It is precisely the speed of cone adaptation which delayed its discovery, because the technical procedure used by Piper and by Nagel and Schaefer and the others was so slow that they missed the major part of the phenomenon almost completely.

If both cones and rods show dark adaptation, then measurements of the eye as a whole should show both phenomena. This was first demonstrated by Kohlrausch (1922) who studied the dark adaptation
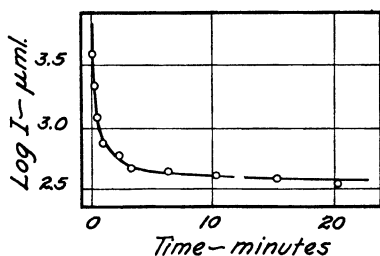

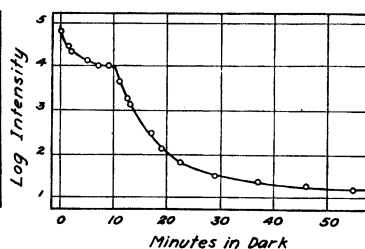Fig. 3   Fig. 4

Fig. 3. Dark adaptation of the fovea as measured with red light. The data are from Hecht (1921), and each point is the average of 30 measurements with 15 observers. Intensities are in micromillilamberts.

Fig. 4. Dark adaptation of the eye as a whole. Measurements of Engelmann's eye made by Piper (1903). Note the presence of cone adaptation and later of rod adaptation.

of a retinal area containing rods and cones, and found that its curve of dark adaptation shows a distinct break, preceding which adaptation is a function of the cones, and after which it is a function of the rods. It is interesting to record that on reëxamination, some of Piper's 1903 measurements, as well as some made later (Piper, 1905b), show this break strikingly, but that it was obscured by the absurd method of plotting adaptation then in vogue. For historical reasons, I give in figure 4 the data for Engelmann's eye taken from Piper's 1903 paper. It is apparent that the primary drop in threshold is rapidly over, as is the case with the foveal cone adaptation in figure 3, while the secondary drop in threshold appears later and proceeds for over 30 minutes.

b. *Separation by color and preadaptation.* If the primary and second-

ary adaptations apparent in figure 4 are really concerned with cone and rod function, it should be possible to isolate them to various extents by means of their visibility curves. Figure 1 shows that with extreme red light the final thresholds of the rods and cones are about the same. Therefore dark adaptation measured with red light will most likely record only cone adaptation since it is the more rapid. On the other hand with blue light, after completion of the rapid cone adaptation, the threshold should continue to drop because of the low level to which the rods finally sink. For colors between these, an intermediate situation is to be expected.
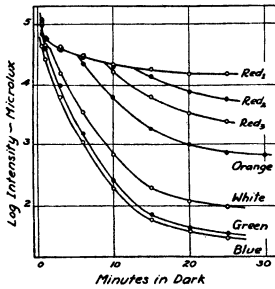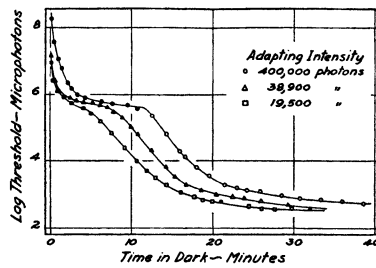

Fig. 5   Fig. 6

Fig. 5. The dark adaptation of an area 1° in diameter, situated 5° above the fovea (Kohlrausch, 1922; 1931b). Red₁ is the only color which limits the measurements to the cones. The other two reds let through more orange light, and show up rod adaptation. With blue light, cone adaptation is barely evident. *Cf.* figure 6.

Fig. 6. The dark adaptation of a 5° field situated 30° nasally (Hecht and Haig, 1936). Though measured with extreme violet light, the course of adaptation shows two distinct sections, due to the high light adaptation preceding the measurements. Note that the secondary, rod adaptation appears later the higher the intensity of preadaptation.

Essentially in terms of these ideas, Kohlrausch (1922, 1931b) investigated the dark adaptation of a small retinal area 5° from the center, using lights of different color. His data are shown in figure 5. It is apparent that for most colors there are two very distinct parts to dark adaptation. The first part corresponds to cone adaptation, and is nearly the same for all the colors which show it. Like the adaptation in figure 3, it is over in about 3 minutes. Soon, however, rod dark adaptation begins to show and, depending on the photochromatic interval, it appears sooner and goes lower as the light moves to the blue.

Kohlrausch's measurements with blue and green light show hardly

any cone adaptation.   This is purely because his preliminary light adap-
tation was not high enough in intensity to bring it out.   Haig and I
(Hecht and Haig, 1936) have recently studied this aspect, and find
that even when measured with extreme violet light, cone adaptation is
strikingly apparent, provided the light adaptation is intense enough.
Our measurements with three different intensities of light adaptation
are shown in figure 6.   It is clear that the higher the light adaptation
the more prominent is the cone adaptation, and the later does the rod
adaptation appear.

Figure 6 is significant in demonstrating the appropriateness of de-
scribing these data in terms of cones and rods.   The filled-in symbols
in the figure indicate that a violet color is apparent at the threshold
during the measurements; if the intensity is reduced below the particu-
lar value indicated, light and color disappear together.   The clear
symbols indicate that no color can be recognized at the threshold.
Evidently, color is always associated with the primary, rapid adapta-
tion which is attributed to cone function, while no color is apparent in
the secondary, slow adaptation attributed to the rods.

The difference in the rates of cone and rod dark adaptation is asso-
ciated with an inverse speed of light adaptation.   Judging by the
measurements of Müller (1931), the rods adapt to a given light intensity
more rapidly than do the cones.

Müller measured the dark adaptation which follows the preadapta-
tion of the eye to white light of 3000 lux for different durations.   His
data are shown in figure 7.   After 1 minute of light adaptation, only
the secondary, rod, dark adaptation is in evidence.   Longer exposure to
the preadapting light apparently changes neither the speed nor the ex-
tent of the rod adaptation, but merely delays its appearance.   Cone
dark adaptation, however, begins to show up only following a 2 minute
preadaptation, and becomes more evident the longer the previous light
adaptation.   Evidently, because of the greater light sensitivity of the
rods, they reach a photostationary state in the light sooner than do the
cones.   These results have very recently been confirmed and extended
in a preliminary report by Wald and Clark (1936).

c. *Separation by retinal location.*   It has long been established
(Schultze, 1866; Rochon-Duvigneaud, 1907; Wolfrum, quoted by Dieter,
1924; Østerberg, 1935) that the histological structure of the human
retina varies in different parts according to a definite pattern.   There
is a central area whose diameter is very nearly 1.5° which is completely
rod-free, while a slightly larger area, 2° in diameter, contains so few rods

that it may be considered practically rod-free.   Outside of this restricted central region, the retina contains rods and cones.   Østerberg (1935) has shown that from the center outward the number of cones per unit area decreases at first rapidly and then more slowly, while the number of rods per unit area gradually increases out to about 18° and then slowly decreases again.   For the greater part of the retina the ratio of rods to cones in an area of given size increases as the area is moved from center outward.

In terms of these histological facts, it follows from the Duplicity Theory that dark adaptation measurements with white light should
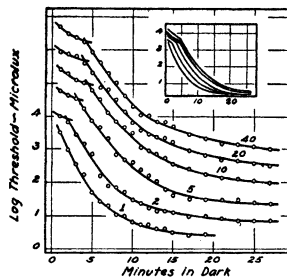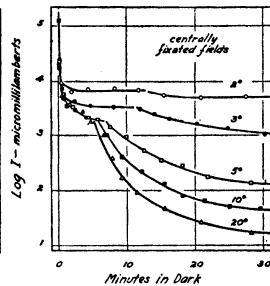

Fig. 7   Fig. 8

Fig. 7. Dark adaptation of the eye after preadaptation for 1, 2, 5, 10, 20, and 40 minutes to 3000 lux (Müller, 1931).   The time axis is the same for all the curves. The ordinates apply only to the lowest curve; for convenience, each series is displaced 0.5 log unit above the other.   The inset brings the data together, and shows that the longer the preadaptation, the more evident is the primary cone dark adaptation, and the more delayed is the secondary rod adaptation.

Fig. 8. The threshold during dark adaptation for centrally fixated areas whose diameters are shown on the data.   The larger the field, the sooner does the secondary rod section appear, and the larger is the intensity range covered by it.   The data are from Hecht, Haig and Wald (1935).

show almost a pure cone behavior when restricted to the 2° central area, and a combination of both rod and cone behavior for larger central areas.   We have recently published measurements (Hecht, Haig, and Wald, 1935) which bear out these predictions.

Figure 8 shows the data secured with a series of centrally fixated areas, using white light for measurements.   With the 2° field, dark adaptation is mainly a foveal cone function, a slight secondary adaptation making itself apparent after about 15 minutes.   For areas larger than 3°, the secondary rod adaptation shows itself unmistakably, the rod thresholds appearing sooner and adaptation going lower as the

area increases.   Beyond 20° there is no very great change with increased area.

The primary cone portions of the curves for areas larger than 2° are not the same as for the 2° field.   This is understandable because as the area increases there are brought into play not only rods but also cones outside the fovea.   It is hardly to be expected that the thresholds and rates of adaptation of these peripheral cones are the same as those of the central cones.

There exists a well-established body of data describing the relation between the area of a field and the minimum intensity required to make it visible (for a summary see Parsons, 1914).   At first glance, therefore, it might seem that the decrease in threshold which shows itself with the larger areas is due to the area-threshold relationship.   However, it is simple to show that the major factor involved in these data of dark adaptation and final threshold has almost nothing to do with area but rather with the fact that the retina is not a uniformly sensitive surface. Coupled with its histological structure already referred to, it possesses a permanently graded sensitivity.

This may be best illustrated in figure 9 which shows the dark adaptation of a 2° field placed in different retinal positions.   In the center at 0° off the central axis, adaptation is essentially cone and, as before, is rapidly over and limited in extent.   Secured at $2\frac{1}{2}$° from the center, the adaptation curve shows the usual rod-cone dichotomy.   The final threshold drops still more as the area is moved out to 5° and 10° from the center.

d. *Night-blindness.*   Hemeralopia is a condition in which vision at low intensities is markedly poorer than normal, and usually becomes manifest to its possessor by his inability to see things in the dim lights at night.   It has been known since ancient days; and from 1881 it has been associated with deficient rod vision (Parinaud, 1881; Treitel, 1885). There are evidently two varieties of night-blindness.   One is temporary; it is caused by a vitamin A deficiency (Holm, 1925; Fridericia and Holm, 1925; Tansley, 1931), and may be cured with cod-liver oil.   Its existence is understandable in terms of the connection between vitamin A and visual purple demonstrated by Wald (1936).   The other variety is inherited (Oguchi's disease in Japan) and is apparently incurable. Probably some other constituent of rod function is missing in this case.

After Piper's first measurements of dark adaptation and their association with rod function, it was natural to think of testing the dark adaptation of night-blind individuals.   This was first done by Hein-

richsdorff (1905) with Piper's apparatus. The conditions for making the determinations, especially the necessity for proper preadaptation to light, were not understood then, and Heinrichsdorff's data are not so obvious as those of Messmer (1908) in which hemeralopes clearly show a diminished dark adaptation; in some cases it is almost completely lacking.

Later, and apparently independently, Takagi and Kawakami (1924) measured the dark adaptation of several cases of hereditary night-blindness and found that for the first two hours in the dark these individuals showed almost no change in threshold, while under the same conditions of measurement the normal eye had dropped in threshold to about
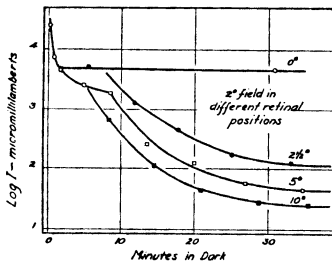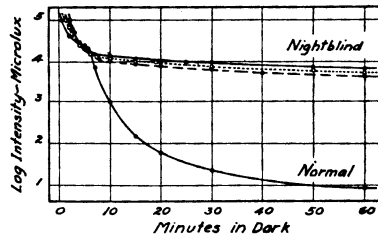

Fig. 9   Fig. 10

Fig. 9. Dark adaptation as measured with a 2° field placed at the different distances from the center recorded on the data. Compare this with figure 8 for centrally fixated fields of different size. The measurements are from Hecht, Haig and Wald (1935). Note that the farther in the periphery the measurements are made, the sooner does the rod section appear, and the lower is the final threshold.

Fig. 10. Dark adaptation of three permanently nightblind individuals, compared with the normal. Data of Dieter (1929). Nightblind dark adaptation evidently shows only primary cone adaptation. Compare this with figure 3.

1/5000 of its initial value in 30 minutes. Rod adaptation seems to have been mainly lost, or at least greatly retarded in speed and reduced in extent. These findings were confirmed by Dieter (1929).

Dieter's measurements are shown in figure 10. They are chosen not because they demonstrate anything fundamentally different from the data of Messmer or of Takagi and Kawakami, but because they were very carefully made with modern apparatus and control and are therefore more precise as data. From them it is apparent that for the first hour at least, dark adaptation of hemeralopes shows only the primary cone drop in threshold and no secondary rod drop. Dieter's evidence is particularly conclusive because he found, under all conditions of brightness, that his hemeralopes possessed only one visibility curve, which

corresponded to his own high intensity, cone visibility curve. This natural experiment therefore bears out the other data, and finds its explanation very simply in terms of the independent functioning of the rods and the cones.

V. INTENSITY DISCRIMINATION. a. *History and meaning.* Measurements of just perceptible intensity differences originally became significant because of their contribution to the problem of intensity recognition. Bouguer (1760), Steinheil (1837), Weber (1834), among others (for summary, see Hecht, 1924b) had shown that the sensory evaluation of intensity differences is relative and depends on the prevailing intensity. None of these data before 1860 could lay claim to any high precision. In fact, it was their very approximate nature which was of significance and which made them acceptable. If I and $I + \Delta I$ are two externally measured intensities which can be recognized as just perceptibly different in sensation, then the data showed that the just perceptible increment ΔI is not an absolute value which produces its sensory effect regardless of the prevailing intensity I, but rather that the two are related so that the ratio $\Delta I/I$ is roughly constant.

The error which came into the study of intensity discrimination,—and which has been perpetuated until this day as the Weber-Fechner Law,—arose when Fechner (1860), on the basis of poor measurements, supposed the fraction $\Delta I/I$ to be rigidly constant. Fechner's supposition of the constancy of $\Delta I/I$ for vision was immediately shown to be erroneous by Helmholtz (1866), even after only a few careful measurements, but it was Aubert (1865) who first demonstrated by extensive measurements with the human eye that $\Delta I/I$ is not constant, but varies in a specific way with I. His results have been corroborated by a variety of workers (see Hecht, 1924b, 1935a) during the last 75 years, not only for the eye but for the ear as well. For the eye $\Delta I/I$ decreases steadily from nearly 1 at low intensities to as little as $1/167$ at high intensities.

The classic research on visual intensity discrimination has been the work of Koenig and Brodhun (1888, 1889) who found, as had Aubert and everyone since, that as I increased $\Delta I/I$ decreased. In addition, however, they found that with further increase in intensity $\Delta I/I$ again rose. This rise at high intensities has been generally accepted, and has formed an essential part of the theoretical explanations (Hertzsprung, 1905; Pütter, 1918; Hecht, 1924b, 1928; Houstoun, 1932) for intensity discrimination in vision.

Very recently the situation has changed fundamentally with respect

to this rise in the fraction $\Delta I/I$ at high intensities.   First, the intensity discrimination of insects, as measured by Wolf (1933a, b) with the bee, and by Hecht and Wald (1934) (see also Wald and Hecht, 1933) with *Drosophila*, shows no rise in $\Delta I/I$ at high intensities; even when tested with intensities 10,000 times higher than the one at which its minimum $\Delta I/I$ becomes established, *Drosophila* showed not the slightest upturn in the value of $\Delta I/I$.   Second, the validity of the upturn for the human eye itself has been seriously questioned by Guild (1932) who showed that the rise appears when the eye is insufficiently adapted to the prevailing intensity, and independently by Steinhardt (1936) who could eliminate it by surrounding the test-field with a large field of about the same brightness as the test-field, and by proper adaptation of the eye to the prevailing brightness.   Indeed, Smith (1936) has just published measurements of intensity discrimination which show not a trace of rise at high intensities.

The upturn in $\Delta I/I$ has been so integral a part of the theories of intensity discrimination that its non-existence has rendered a new formulation necessary for the data (Hecht, 1934b; 1935).   The new treatment describes all the available data including some measurements (Wright, 1935; Hecht, 1936; Smith, 1936) specifically designed to test it.   Theory apart, however, the data themselves show a basic similarity for all animals studied, and furnish an interesting corroboration of the Duplicity Theory for the human eye.

b. *Insects, clam and man.*   Intensity discrimination has been measured in insects, in *Mya*, and in man.   The data for *Drosophila* are in figure 11.   They are from the work of Hecht and Wald (1934) and were determined by the method of moving stripes used by Hecht and Wolf (1929) for measuring visual functions of animals with eyes.   They represent the average measurements with 24 flies, and show that $\Delta I/I$ steadily decreases as I increases.   The relation between the two is continuous, such as would be expected if just one photoreceptor system were concerned.   The same is true for the data with the bee. Wolf's (1933a) first measurements with the bee are shown as solid circles in figure 12, while his later measurements (Wolf, 1933b), which are smoother, more numerous, and obviously more critical, are shown by clear circles.   Though they were made with different sizes of stripes, the measurements are all essentially similar, and indicate most likely that only one set of photoreceptors is present.

Drosophila and the bee have organized eyes.   The only other data of intensity discrimination available for invertebrates are for the clam

Mya, which has a diffuse sensitivity to light all over its siphon. The measurements with *Mya*, made twelve years ago (Hecht, 1924c), record the necessary fractional increase in illumination to which the animal responds with a specific reaction time, after having been adapted to a given intensity. Figure 13 shows the data for responses at five different reaction times. The measurements are not so smooth as can
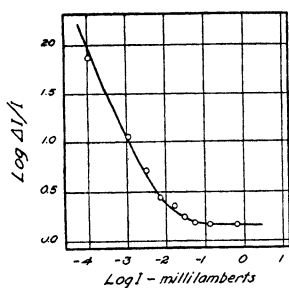

Fig. 11   Fig. 12

Fig. 11. Intensity discrimination of *Drosophila* (Hecht and Wald, 1934). The points are the averages from 24 flies. The curve drawn through the data is from equation (10) derived in section IX.
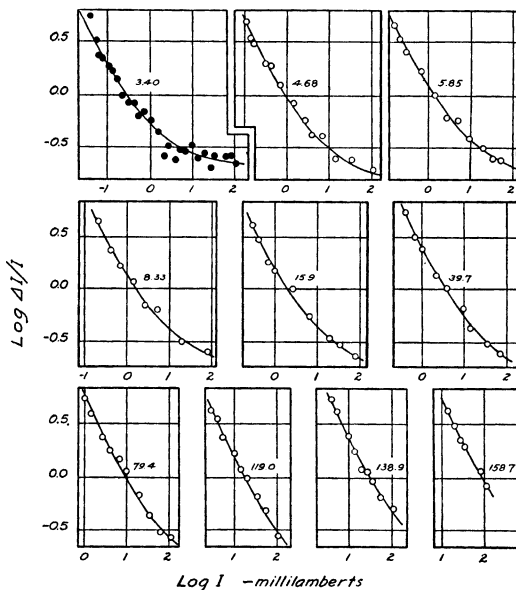
Fig. 12. Intensity discrimination of the honey bee (Wolf, 1933a; b). The black circles are the data from the first paper; the plain circles from the second paper. The numbers attached to the curves are the visual acuities multiplied by 1000 and are inversely proportional to the size of the stripes used for the measurements. The same curve is drawn through all the data; it is from equation (11) derived later.

be wished, but they are consistent in showing that the relationship of $\Delta I/I$ to I is the same for all reaction times, and that it is a single function.

The remaining measurements of intensity discrimination are for the human eye, and when freshly examined two years ago (Hecht, 1934b) gave an unexpected demonstration of the separateness of rod and cone function. For their historical interest the earliest intensity discrimina-
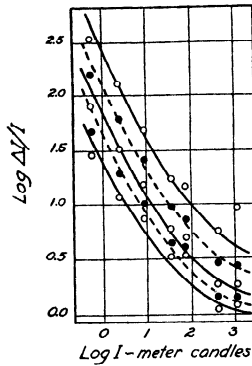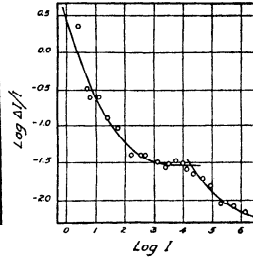
Fig. 13   Fig. 14

Fig. 13. Intensity discrimination of the clam, *Mya*, from the measurements of Hecht (1924c). The clear circle so obviously off the topmost data is an extrapolated value. The curves are all from equation (11) derived later in this paper.

Fig. 14. Aubert's measurements of the intensity discrimination of his own eye. The intensities are those given by Aubert (1865). Judging by his description, they should be divided by 500,000 for conversion into millilamberts. The data obviously break into two sections representing rod and cone functions.
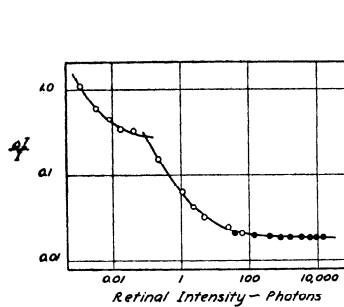

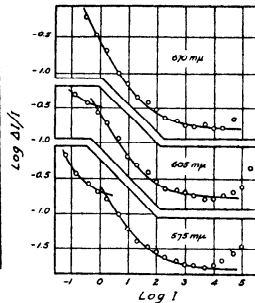Fig. 15   Fig. 16

Fig. 15. Intensity discrimination of the human eye. The measurements of Blanchard (1918) are the plain circles; those of Lowry (1931) are the black circles and have been raised 0.15 log unit along the ordinates to bring them into continuity with Blanchard's data. Note the natural breaking of the data into two sections indicative of rod and cone functions. The curve for the high intensity, cone data is from equation (11); the one for the rod data is actually from equation (10), but the other equation would do just as well. The equations are derived in section IX.

Fig. 16. Intensity discrimination for Koenig's eye with red, orange, and yellow spectral light (Koenig and Brodhun, 1888). The red data are continuous and show only cone function, whereas the orange and yellow show increasing amounts of rod function. As in figure 15, the curves are from equation (10) for the rod section and from (11) for the cones.

tion measurements (Aubert, 1865) are shown in figure 14.   The points
are single measurements and are fairly rough, but their significance is
unequivocal.   The data clearly range themselves into two parts as
would be expected if they represent the behavior of two photoreceptor
systems.   That this phenomenon is not an isolated one is demonstrated
in figure 15 which shows the measurements of Blanchard (1918) as open
circles, and of Lowry (1931) as solid circles, both having been made in
the same laboratory but thirteen years apart.   The data break into two
parts, of which the low intensity section is most likely concerned with
rod function, while the high intensity section expresses cone function.

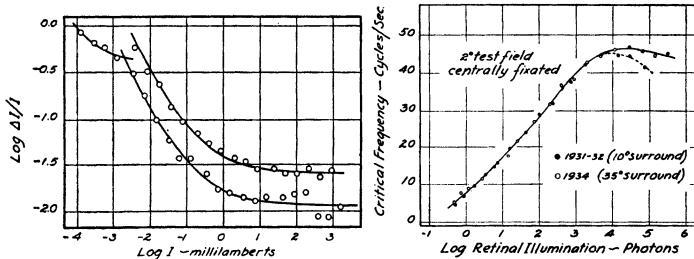Fig. 17   Fig. 18

Fig. 17. Intensity discrimination with different retinal areas, and with white
light (Steinhardt, 1936).   The upper data are with a field 56' in diameter; the lower
with a field 3°44' in diameter.   The upper data show only cone function and are
described as usual by the curve from equation (11).   The lower data show both
rod and cone function; as in figures 15 and 16 the curve through the former is from
equation (10), while through the latter it is from (11).

Fig. 18. Critical frequency and illumination.   The data show a comparison for
the same eye (S. H.) using central fixation and a 2° flickering field, between meas-
urements made several years apart with a 10° surround (Hecht and Verrijp,
1933b) and with a 30° surround (Hecht and Smith, 1936).

c. *Color and position.*   The two features which we have used in dark
adaptation for distinguishing rod function and cone function are their
differences in spectral sensibility and their differences in retinal location.
These two characteristics are similarly useful in intensity discrimina-
tion.   In terms of the visibility curves already shown in figure 1, we
should expect that when the relation between $\Delta I/I$ and the intensity is
measured with extreme red light, only the cone function should be
apparent and the data should be continuous as they are with *Mya* and
the insects.   With orange light, however, we should expect the addi-
tional appearance of a small rod section, and this rod section should be
larger as the spectrum goes toward the blue.

Koenig and Brodhun (1888) made measurements of $\Delta I/I$ with dif-

ferent spectral colors, and their data for red, orange, and yellow are reproduced in figure 16. No break is apparent for the data of 670 mμ, but a break is clearly shown in the 605 mμ and in the 575 mμ data. The low intensity section is small for the orange and large for the yellow. As already pointed out, the few points at high intensities showing a rise in $\Delta I/I$ must be disregarded because they were undoubtedly made under conditions which did not prevent the appearance of a rise.

The second method of demonstrating the separateness of rod and cone function is by measurements with differently located retinal areas, and has been used by Steinhardt (1936). For white light and test areas larger than 2°, his measurements without exception fall on a double curve similar to the data of Blanchard and of Aubert, while for smaller, foveally fixated areas they always form single curves like those of Koenig and Brodhun with light of 670 mμ. Figure 17 shows two examples of his data. The upper measurements are for white light and a test area 56′ in diameter having a large surround in order to maintain the eye as a whole to the prevailing intensity of the measurements. This size of test field falls entirely within the rod-free area of the fovea and, as a result, the measurements show no inflection point. The lower data in figure 17 were made with a field 3°44′ in diameter, also with a large surround, and show clearly the presence of a break indicating the existence of two separate functions,—rods at low intensities, and cones at high intensities.

Smith (1936) has recently published measurements of $\Delta I/I$ using fields of 20′ diameter, the two halves of which are separated by distances varying from 4′ to 30′, and in one case placed in separate eyes for binocular judgment. Judging by the field sizes, all his measurements fall in the rod-free area of the retina and, as expected, do not show any trace of discontinuity. The data thus corroborate Steinhardt's findings and support the general thesis of rod and cone identification.

VI. INTERMITTENT STIMULATION. a. *Nature of problem.* The relation between visual function and the Duplicity Theory is nowhere so well illustrated as in the history and data of flicker. This is particularly apparent because this field of knowledge has undergone a rapid development and organization in the last few years.

The flickering sensation produced by regularly interrupted illumination disappears when the frequency of interruptions is made sufficiently high. The precise point at which flicker disappears is known as the critical fusion frequency, and may be determined with considerable accuracy. As a result, its value has been shown to depend on a variety of conditions.

The most basic factor which controls the critical frequency is the

intensity. Though the dependence of the critical frequency on illumination was recognized over 100 years ago by Plateau (1829) and is evident from the work of Emsmann (1854) and of Nichols (1884), it was only 45 years ago that Ferry (1892) formulated what has since become known as the Ferry-Porter Law, namely, that the critical frequency is proportional to the logarithm of the illumination intensity. Ferry's published measurements support this formulation only in the most general way, but the later data of Porter (1902) are adequate for its statement.   Porter's work was corroborated by Kennelly and Whiting (1907), by Ives (1912), and by Luckiesh (1914).

Porter found that when the critical fusion frequency—as cycles of light and dark per second—is plotted against the logarithm of the intensity, the data fall on two straight lines instead of one.   The two lines intersect at an illumination of about 0.25 meter candle, and the slope of the lower is 1.56 while that of the upper is 12.4.   These findings were confirmed by Ives (1912a), whose data for different parts of the spectrum also show a dual logarithmic relation.   However, the slope of the straight lines and their point of intersection seem to vary with the wavelength of the light, the upper and lower limbs of the relationship varying in different ways.   In addition, Ives found the extraordinary fact that for blue light the lower line becomes horizontal.

These peculiarities are difficult to reconcile with the obvious interpretation of Porter's data in terms of the Duplicity Theory, and this difficulty has been emphasized by Allen (1919, 1926) who has drawn through his measurements about five short, straight lines of different slope instead of the usual two.   Judged by their experimental error, the data presented by Allen do not justify this treatment; the points most probably lie on a continuously curving line.   The work of Lythgoe and Tansley (1929) distinctly gives no support to Allen's multiplicity of straight lines.

Lythgoe and Tansley's measurements confirm the logarithmic relation of intensity to fusion frequency, but Lythgoe and Tansley attach no importance to its strict formulation as done by Ferry, by Porter, and by Ives, and consider that their data agree only under certain conditions with the linear relation of critical frequency to $\log I$.   The same may be said about the measurements of Granit and Harper (1930), who found that for a range of about 1 to 1000 in intensity the critical frequency is very nearly directly proportional to the logarithm of the intensity. For higher intensities the relationship does not hold, and the curve of frequency against $\log I$ tends to become horizontal, as already found by Grünbaum (1898).

One striking thing appears in the work of Lythgoe and Tansley though they do not recognize its significance. Ives had found that for blue light the lower limb of his data is horizontal, and in this he had been confirmed by Allen. This seemed a special property of blue light. However, Lythgoe and Tansley have recorded that when measurements are made with a retinal area 10° from the center of the eye the lower portion of the data tends to be horizontal even for white light.

As a result of these researches, it might seem that flicker data make no sense in terms of the Duplicity Theory. In fact, it was precisely this confusion which prompted me originally (Hecht and Verrijp, 1933b) to study flicker; this, and the fact that none of the measurements existing at the time covered a range of intensities sufficient to define the relation between critical frequency and intensity over the functional range of the eye. Since then, we have measured this relation for different portions of the retina, for different sizes of field and for different colors, for as large a range of illuminations as possible, and under such conditions of fixation and surrounding illumination as to render the data reproducible and definitive. As a result the confusion has disappeared, and the conflicting data have become integrated into a scheme which is consistent with the visual knowledge already presented and understood.

b. *Central and peripheral measurements.* We may again use the type of thinking and experimentation which the previous sections have shown to be valid in differentiating between rods and cones. If the separation of rod and cone function first suggested by Porter's data is correct, it should be possible to isolate them in the usual way,—first, by studying different retinal areas, and second, by means of spectral illumination. Judging by the distribution of cones and rods, the relation between fusion frequency and intensity, as measured with central areas smaller than 2° in diameter, should be a continuous function representing cones, whereas with larger areas or with similar small areas outside the fovea, the relation should show a duplex character illustrative of the predominant working of rods at low intensities, and of cones at high intensities.

The measurements of Hecht and Verrijp (1933b) with a small field located centrally and peripherally show this to be correct. Figure 18 shows two sets of measurements on my own eye, made several years apart (Hecht and Verrijp, 1933b; Hecht and Smith, 1935; 1936), with a 2° field situated in the fovea. The data demonstrate that for the fovea there is one continuous relation between critical frequency and the logarithm of the intensity. The relationship is distinctly sigmoid, the S-shape being rather drawn out. In the middle range of intensities, the

data lie with reasonable precision on a straight line, and thus confirm
Porter, Ives and the other workers, even to the extent of having a slope
of the same magnitude as found by them.

Below the middle range the data form a gentle curve which stops
fairly abruptly when with central fixation the field appears uniform even
when the test area is extinguished.   At the highest intensities the rela-
tion between critical frequency and log I rapidly ceases to be linear.
The curve flattens out, and as with intensity discrimination, remains
flat provided the adaptation and surround are adequate.

Using the same sized field (2° in diameter with a non-flickering 10°
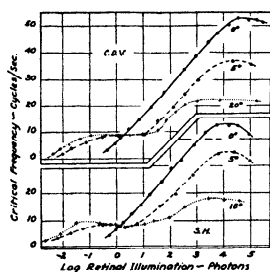surround), we measured the relation between critical frequency and in-
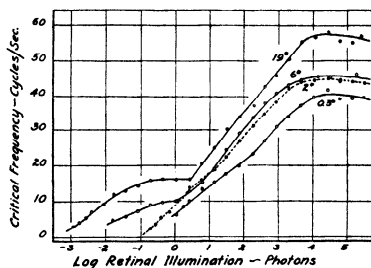

Fig. 19   Fig. 20

Fig. 19. Relation between critical frequency and log I for white light with a 2°
field in four retinal locations: at the fovea, and at 5°, 15° and 20° above the fovea.
The data are from Hecht and Verrijp (1933b).   Due to an error in the original
paper, the intensities have had to be multiplied by 40 to convert them correctly
into those here given.

Fig. 20. Influence of the area of test field on the relation between critical fre-
quency and log I (Hecht and Smith, 1936).

tensity at 5°, 15°, and 20° from the center.   The results are shown in
figure 19, and are strikingly different from the central data in that they
clearly fall into two parts.   The first is at low intensities, where the
critical frequency first rises with log I and then reaches a maximum
which is maintained approximately constant for about 1.5 logarithmic
units.   The total intensity range covered by this rise and plateau is
about 3.5 logarithmic units.   The second part also begins with a rise
in critical frequency as log I increases, and also terminates when the
critical frequency reaches a maximum.   The intensity range covered
by the second part is about 4 logarithmic units.   The same results ob-
tain in whatever peripheral direction of the eye the measurements are
made.

Since the central, 2° field falls within the relatively rod-free area of the retina, the continuous nature of the data mark them as a function of the cones alone. The double nature of the peripheral measurements very likely represent rod function for the low intensity section and cone function for the high intensity section. This is borne out by the increasing separation of the two sections as measurements are made farther and farther from the center: the cone section shifts to higher intensities and the rod section to lower intensities, as would be expected from the increasing ratio of rods to cones in these regions.

We have very recently measured the relation between critical fusion frequency and intensity for four centrally located areas 0.3°, 2°, 6°,
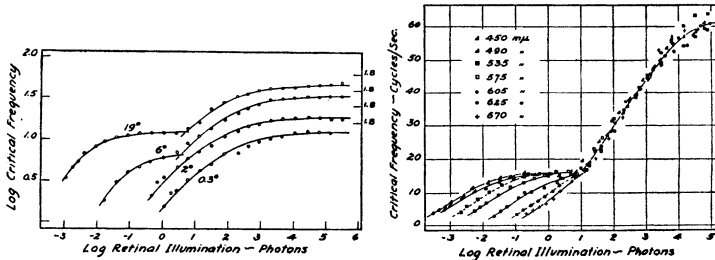

Fig. 21   Fig. 22

Fig. 21. Area and the flicker relation. The log I axis is the same for all the data. The numbers on the log frequency axis to the left apply to the uppermost data only; the other data have been moved down in steps of 0.2 log unit in order to space them, and their precise position is given on the right. The curves are from equation (14) in which for the cone portions $m = 2$, $n = 2$; and for the rod portions $m = 2$, $n = 1$. Cf. figure 29 shown later.

Fig. 22. Critical frequency and log I for different parts of the spectrum for the eye of S. H. (Hecht and Shlaer, 1936).

and 19° in diameter, and our measurements (Hecht and Smith, 1935; 1936) confirm these conclusions. The data for E.L.S. are in figure 20 and, as expected, those for 6° and 19° break sharply into a rod and cone section, while the 2° and 0.3° fields fail to show the rod section. The slight bend in the latter data need not concern us here; it is certain that the bend is not due to a slight admixture of rods.

The data for the 6° and 2° fields are of pointed interest in the problem of flicker and area. Except for the absence of the rod piece in the smaller field, the two sets of data are almost identical. Under the circumstances of possessing the same surround, a ninefold increase in area of the test field hardly changes the relation of critical frequency to in-

tensity so far as cone function is concerned (*cf.* Granit and Harper, 1930).

Figure 21 presents the data of S.H. as the logarithm of the critical frequency against the logarithm of the intensity. This type of plot shows more strikingly the phenomena already described. In spite of the irregularity in the 0.3° data, a single curve describes the measurements fairly well. The same single curve is even more expressive of the 2° data, and it is also drawn through the cone portions of the 19° and 6° data.

The rod sections of 19° and 6° require a slightly different curve which is the same for the two fields. It is worth emphasizing that the rod sections of the two large fields have the same curve drawn through them. While this is not clearly seen in an ordinary graph of critical fusion frequency against $\log I$, it becomes plain in the $\log I - \log f$ plot of figure 21. This is because on a $\log I - \log f$ plot of this kind the shape of the curve relating critical frequency and intensity is invariant and uninfluenced either by the intensity units or by the absolute values of the critical frequency, since these merely shift the position of the curve on the two axes. The same is true of the curves shown in the section on intensity discrimination. The identity of the curves for 19° and 6° shows that the difference between them is not basic, but merely represents a change in one of the constants in the equation which describes them.

Exactly the same is true for any systematic differences which the cone data show. Fundamentally the systems in the rods and cones which determine the relation between critical frequency and intensity remain the same regardless of area. Only the parameters are altered by changing the area. This has finally been recognized by some of the investigators who are interested in studying the influence of various factors on visual functions. For example, Smith (1936) who was essentially concerned with synaptic and other nervous influences on intensity discrimination has found that the fundamental intensity discrimination relation remains unaltered, and that the best way to describe these various nervous influences is to record their effects on the parameters of the basic equations (Hecht, 1934a, 1935) for intensity discrimination. The same thing is clearly possible with flicker, and should be done before the determination of fusion frequency is rushed into medicine for use as a clinical method (Granit, 1936).

c. *Spectral data.* In order to confirm the identification of the two sections shown by the measurements which include the periphery, we

have used different parts of the spectrum to study the relation of critical frequency to intensity. It is worth looking again at figure 1 in order to see what may be expected. Spectral energy can produce no visual effect until it reaches the relative intensity indicated by the rod curve. Above that, rod function dominates until the cone threshold is reached. The intensity distance over which the rods dominate in visual function changes throughout the spectrum: between 670 and 630 mμ it is small and alters only slowly; beginning at about 600 mμ and going toward the blue the distance becomes rapidly larger, while below 500 mμ it remains practically constant.

Preliminary investigation (Hecht and Verrijp, 1933a) showed these expectations to be correct. We therefore measured in detail (Hecht and Shlaer, 1935; 1936) the relation between intensity and critical frequency for different parts of the spectrum with a circular test field 19° in diameter, surrounded by a non-flickering area 35° in diameter.

The information conveyed by the measurements can best be understood from their graphic representation. As figure 22 shows, the data break sharply into two sections. The high intensity portions, identified with cone function, fall together for all the colors. The low intensity sections, identified with rod function, are spread out much as expected and extend to lower and lower intensities with decreasing wavelength.

The separation between rod and cone sections for white light shown in figure 20 almost coincides with that for 535 mμ (yellowish-green). The separation for white light is dependent in part on the integrated spectral sensibilities for rods and cones, and in part on their absolute thresholds. Wolf and Zerrahn-Wolf (1936) have just reported critical frequency measurements for the sunfish *Lepomis* used by Grundfest (1932b) for his spectral visibility studies. Just as Grundfest found two visibility curves, so Wolf and Zerrahn-Wolf find two limbs to the flicker data indicating rod and cone function. The intensity separation of the two limbs is more than 4 log units, the main rod section being almost impossible to measure because it lies below the threshold of human vision.

Figure 22 resolves the mystery of Ives' old measurements showing that the low intensity portions of critical frequency data which he found for different parts of the spectrum may be represented by straight lines which differ in slope, the red being steepest and the violet being practically horizontal. It is apparent in figure 22 that for short stretches near the rod-cone transition, straight lines can be drawn through the rod data, showing different slopes for the different wavelengths.

The real phenomenon, however, is something quite different. It is that the separation of rod and cone sections as a whole increases as the wavelength decreases. This is shown strikingly by figure 23, in which the data of S.S. are plotted as the logarithm of the critical frequency against the logarithm of the intensity. The data for 670 mμ fall on a single, continuous curve, whereas the data for all other parts of the spectrum are best described by two separate curves. The transition between the two portions is quite sharp for all but the blue and violet
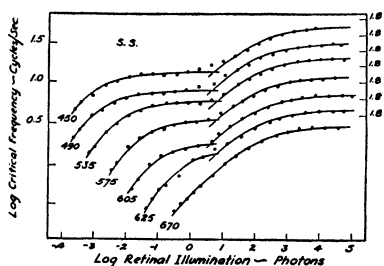
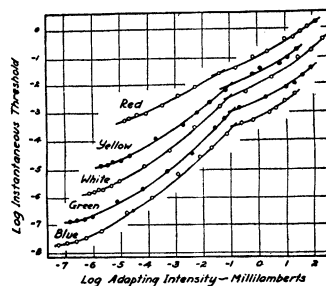

Fig. 23   Fig. 24

Fig. 23. Critical frequency and intensity for different spectral regions for the eye of S. S. (Hecht and Shlaer, 1936) plotted as log frequency against log intensity. The numbers on the ordinates to the left apply to the topmost data; for convenience, the others have been moved down in steps of 0.2 log unit, and their exact positions are indicated to the right. The curves are from equation (14) in which for the cone portions $m = n = 2$, and for the rod portions $m = 2$, $n = 1$.

Fig. 24. Relation between adaptation intensity and instantaneous threshold for different colors (Blanchard, 1918). The adapting intensity axis is the same for all the data. The numbers on instantaneous threshold axis apply only to the data for white light. To avoid confusion the yellow data have been displaced upward 0.5 log unit; and the red 1 log unit; the green downward 0.5 log unit; and the blue 1 log unit. Actually the high intensity portions of all the colors practically coincide, whereas the low intensity sections drop more and more from the red down.

data. The high-intensity, cone curve is in the same position for all colors, and the only effect of changing the spectral composition of the light is to shift the position of the low-intensity, rod curve along the intensity axis without in the least changing its form.

The identification of rod and cone function is borne out by subjective observation. At low intensities and below the critical fusion frequency the flicker is distinctly located in the peripheral portion of this 19° field so that the field resembles a flickering doughnut, and the last appearance of flicker is always in the periphery. With increasing inten-

sity the first sign of approaching cone function is the appearance of color in the field, which becomes identifiable with certainty about 0.5 log unit below the actual inflection point of the measurements.

At the intensities around the transition, two separate loci of flicker are very often apparent near the critical frequency: one in the periphery, and the other in the center. At intensities higher than the transition intensity but near it, flicker usually persists longest in the center, but beyond these intensities the last trace of flicker may be in any part of the field. Obviously the rods determine the low intensity section and the cones the high intensity section, but the specific cones which set the critical frequency are not necessarily the same throughout the high intensity section. At the highest intensities, the last appearance of flicker in making a measurement is usually in the center of the field.

VII. INSTANTANEOUS THRESHOLD. One of the interesting things about the application of the Duplicity Theory to various visual functions has been its unexpected illumination of data which, though well known, have remained obscure in their interpretation and neglected in their relation to the rest of the field. A case in point is Aubert's data of intensity discrimination which have been known for about 75 years and have been frequently quoted, but were never recognized as demonstrating the Duplicity Theory until now. I myself had studied these data many times, but never saw their separation into rod and cone sections until in 1934 when I plotted them as $\log \Delta I/I$ against $\log I$, as shown in figure 14. Under these circumstances the division almost leaps out from the data by itself. The same thing happened with Blanchard's measurements shown in figure 15, and with those of Koenig and Brodhun in figure 16.

An even more curious situation concerns the data of Blanchard (1918) on instantaneous thresholds. Blanchard's measurements were of the following kind. The eye is adapted to a given intensity by looking for some time at a large, suitably illuminated area. At a specific moment this adapting light is cut off with a shutter, and at the same time the minimum intensity is determined at which a centrally-fixated, 5° area becomes visible instantaneously. This naturally requires several trials, each preceded by proper adaptation, until the precise threshold intensity is found which renders the central area just visible immediately after the adapting light is shut off.

Blanchard made these measurements over the whole range of visually effective intensities, using white light as well as the red, yellow, green, and blue portions of the spectrum isolated by roughly monochromatic

filters. He found that the instantaneous threshold intensity increases with the adapting intensity, and that on a double logarithmic plot "the curve for white light is seen to be practically a straight line with the exception of the extreme intensities, and may be represented over this region by the" appropriate equation for a straight line. He says further that "the curves for the different colors are very similar to that for white, the instantaneous thresholds being nearly equal for moderate brightnesses and diverging most for the lowest brightness," and correctly attributes the latter fact to the Purkinje phenomenon.

Blanchard adds the pertinent observation that "all the color curves except red show a decided dip, indicating a depression of sensibility, in a region roughly between 0.01 and 1 milliambert, a region corresponding to about the average range of interior brightnesses at night," but fails completely to appreciate the meaning of his observation. I have replotted his data in figure 24, from which the significance of his "dip" is at once apparent in terms of the Duplicity Theory.

With red light the measurements show almost a continuous function. When plotted by themselves the red data may easily be fitted with one line, as were those of intensity discrimination in figure 16 and of flicker in figure 23. In fact I did precisely this even while making the first draft of figure 24 for the present paper.   It is only when the data for the other colors are added that the double nature of the function becomes apparent, because the inflection point in the red data, though gentle, corresponds so obviously with the point of striking change in slope shown by the yellow, white, green, and blue data.   Judged by the transmission data published by Blanchard, his red light included the spectrum beginning at 600 mμ; it would therefore be expected to stimulate the rods as well as the cones in this 5° centrally-fixated area.

Figure 24 shows that the high intensity portions for all the colors and for white are much the same, indicating their common origin in cone function.   Except for the red, the low intensity sections drop sharply away also in a form which is approximately the same for all the measurements.   Note particularly that the low intensity rod section is largest for blue light and becomes smaller through the spectrum to the red, as is to be expected from the sensibility curves in figure 1.   Considering all that has already been said about similar things in dark adaptation, intensity discrimination, and flicker, it is hardly necessary to labor the point of these data.

VIII. VISUAL ACUITY.   a. *Normal eye.*   The last function to be considered in relation to the Duplicity Theory is the resolving power of the

eye and the influence of illumination intensity on it.   A measure of the capacity of the eye for resolving the details of its environment is visual acuity.   This is defined as the reciprocal of the angular distance which must separate two contours in order that they may be recognized as discrete, the unit of separation being a minute of arc.   The relation between visual acuity and illumination was first investigated in 1754 by the astronomer Tobias Mayer.   He believed that he had found that visual acuity increases as the sixth root of the intensity of illumination.

Since Mayer, many investigators have tried to find the exact nature of the relationship between visual acuity and illumination.   Uhthoff (1886), who reviewed the data 50 years ago, records about twenty contributions to this particular phase of vision.   Most of these data cover only a very small range of illuminations, and therefore merely confirm daily experience.   Nevertheless, even a small range enabled Posch (1876) to conclude that visual acuity varies very nearly as the logarithm of the illumination intensity.   This relation is borne out by the more comprehensive data of Klein (1873) and Cohn (1883), though neither of these authors drew such a conclusion.

Uhthoff (1886; 1890) himself investigated the matter further by using white and colored lights covering a great range of illuminations.   From his data it is apparent that in a general way visual acuity varies in proportion to log I; the relation between the two is not strictly rectilinear, but sigmoid.   His data are excellent, and were confirmed and extended in great detail by Koenig (1897) whose measurements have since become classic.

Since Uhthoff's and Koenig's experiments the number of people who have measured this relationship is not large.   Up to 1912 they are recorded in an excellent memoir by Löhner (1912); an earlier review is by Zoth (1905).   After that, none of the contributions (Rice, 1912; Roelofs and Zeeman, 1919; Ferree and Rand, 1923; Lythgoe, 1932; Wilcox, 1932) have covered the range of illumination necessary for a complete statement of this function of the eye.   They all indicate, however, that the relation between visual acuity and illumination is of the general form found by Koenig.

In 1926 I made an interpretation of these data (Hecht, 1926, 1928) in terms of certain photochemical and statistical notions which accounted for the precise form of the relationship.   As a result of these ideas, it became necessary to know the influence of intensity on visual acuity for animals other than man.   Such studies were soon forthcoming (Hecht and Wolf, 1929; Hecht and Wald, 1934; Clark, 1935),

and showed that for all animals the general form of the relationship is much the same as for man.

From the point of view of rod-cone function, it is not necessary to know the precise form which the data for the human eye assume. The significance of Koenig's data in this connection is clear enough, and was to a certain extent recognized by him as well as by von Kries (1929). However, their full value for the separation of rod and cone function becomes apparent only when they are plotted in a double logarithmic grid as in figure 25, since in this way the lower values of visual acuity receive their share of importance, and the experimental error as a percentage is of the same magnitude throughout.
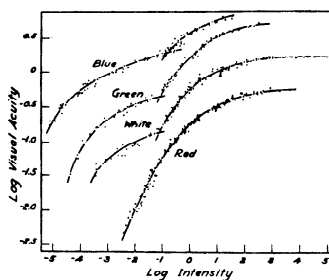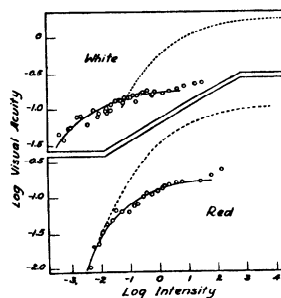

Fig. 25   Fig. 26

Fig. 25. Visual acuity and illumination for different colors (Koenig, 1897). The intensity axis is the same for all the colors. The numbers on the visual acuity axis apply only to the data for white light. For convenience in showing the data, the red measurements have been displaced downward 0.5 log unit; the green, 0.5 log unit upward; the blue, 1 log unit upward. The separation of the data into two sections needs no emphasis.

Fig. 26. Visual acuity and illumination with red and white light for a completely colorblind person (Koenig, 1897). The white curve and the red curve from the normal data of figure 25 have been drawn in for reference.

From figure 25 it is apparent that with red light there is only one continuous relationship between visual acuity and intensity, while for white, green, and blue there are two relationships, one at high intensities and the other at low intensities. Koenig had considerable difficulty with blue light and could not complete the measurements at high brightness and high visual acuity. The high intensity limb for all the colors is the same as for red and must therefore represent cone function; by the same token the similarity of the low intensity portion for blue, green, and white, and its complete absence in the red, mark it as the expression of rod function. Note particularly the position on the intensity axis

and the relative size of the rod portions for blue, green, and white. The blue section is largest, the green next, the white next, and the red is non-existent, due to the movement of the rod section along the intensity axis, as in figure 5 for dark adaptation and in figure 23 for flicker.

b. *Complete colorblindness.* Koenig recognized the implications which his visual acuity measurements have for rod and cone behavior because his work was done almost immediately after von Kries had reintroduced the idea of duplex function into visual physiology. Koenig realized that in a completely colorblind individual the upper part of the data should disappear and leave only the lower limb plus any extensions of it. He accordingly investigated the visual acuity of a completely colorblind person, using white and red lights.

The data he secured are given in figure 26 and are plotted on the same grid as the normal data. Included for comparison in figure 26 are the curves for the normal eye for white and red taken from figure 25. With white light the data for the colorblind fall right on the rod portion of the normal curve. In addition they extend continuously beyond the point of inflection which in the normal curve indicates the entrance of the cones. There are a few points at the highest intensities with white and red light for the colorblind which may perhaps indicate a rudimentary cone function.

The data for red light are particularly revealing. They have much the same shape as the rod portions of the blue, green, and white data for the normal eye. But they suffer a shift along the intensity axis as do the rod data of the red flicker measurements in figure 22, and end up just to the right of the normal red data, being coincident with them at the lowest intensities. In figure 26 the position of the colorblind red data under and to the right of the normal data explains why the normal red curve is continuous and without a break. It is not that the rods do not function in red light; it is that in red light the cones have about the same intensity thresholds as the rods (*cf.* fig. 1); but since the cones are closer together in the fovea than are the rods in the periphery, they can resolve smaller distances and therefore dominate the measurements by recording the correspondingly higher visual acuities.

The dominating characteristic which differentiates rod and cone function in visual acuity is obviously purely anatomical. For other visual capacities the dominating differentiation may be quite different and may depend on the properties of the photoreceptor mechanism. In dark adaptation it is very likely the speed of the regenerating chemical process which serves to separate rods from cones in the measurements. For

intensity discrimination and flicker it may be the difference in the just effective photochemical change in the receptor cell. No matter what the basis for the particular difference in rod and cone function happens to be, it gives expression to the spectral sensibility curves and becomes revealed in the measurements.

IX. THE NATURE OF THE PHOTORECEPTOR PROCESS. a. *The stationary state.* The first purpose of this paper has been to show that the various visual functions which have been measured with precision fall quite simply into the design of the Duplicity Theory. This objective has now been accomplished, and has involved little more than the presentation of the data themselves. The second purpose is to go somewhat deeper into the quantitative meaning of the measurements, and to consider their relation to the processes which probably occur in the rods and cones when they are activated by light.

The most general ideas that one can have about the photoreceptor process involve three things. *a.* There has to be a sensitive substance which absorbs light and is changed by it into one or more active products. *b.* It is necessary to maintain a supply of this photosensitive material; otherwise it would be used up and the process would come to an end. These two processes may be called the primary light and primary dark reactions. *c.* The active photoproducts of the primary light reaction must do something of which the end result is an impulse from the receptor cell. This is the secondary dark reaction.

These three requirements are the minimum essentials. The photoreceptor process is certainly more elaborate. Moreover, vision and light sensitivity involve not only the receptor process in the sensory elements but the nerve impulses generated by the stimulated elements and by neighboring elements, as well as all sorts of central nervous changes of which we know little or nothing. Since these are all concerned with vision, they surely influence its characteristics to some extent. However, no matter what determines the nature of vision, the ultimate place of origin of the impulses passing up the optic tracts is in the action of light on the sensory elements. Therefore the various properties of vision and photoreception must owe some of their quantitative form to the characteristics of the reactions which take place between light and the sensitive elements. It is obviously of first rate biological interest to discover how close this correlation is.

Consider the properties of the simplest photochemical system which can be suggested as corresponding to the primary light and dark reactions. Let there be a photosensitive substance whose total initial con-

centration is a; let light of intensity I shine on it; let the concentration of photoproducts at the moment t be x; and let it be assumed that some of these products reunite by themselves or with the help of additional substances to form again the sensitive material. The velocity of the process as a whole will then be

$$(dx/dt)_I = k_1 I (a - x)^m - k_2 x^n \tag{4}$$

where m and n represent the order of the primary photochemical reaction and of the primary dark regenerating reaction respectively; and k_1 and k_2 are their velocity constants, k_1 including the absorption coefficient. The intensity enters as the first power because this is the only assumption compatible with Talbot's law (Arnold and Winsor, 1934), as well as with ordinary absorption ideas as shown in equation (3) in the third section of this paper.

On continuous illumination corresponding to the adaptation of the eye to a constant intensity of light, such a photochemical system reaches a stationary state in which the opposing reaction rates become equal; the concentrations of sensitive material and photoproducts become constant; and equation (4) becomes equal to zero. This gives

$$KI = x^n/(a - x)^m \tag{5}$$

where $K = k_1/k_2$ for convenience.

Equation (5) describes the photostationary state set up by light in terms of the simplest chemical ideas about the primary light and dark reactions. Examination of the data reveals that intensity discrimination, visual acuity, and flicker all depend on light intensity as if they were determined by the conditions at the stationary state described by equation (5). In fact, so close is the relation between the equation and the data, that it is possible to determine from the data the precise values of m and n in the equation.

b. *Intensity discrimination.* When the eye is exposed to light of intensity I, the combined rate of the primary light and dark reactions in the photoreceptor process is that given by equation (4). At complete light adaptation to this intensity the velocity becomes zero, and the equation becomes.

$$I = k_2 x^n/k_1 (a - x)^m. \tag{6}$$

If the system is now exposed to intensity $I+\Delta I$, which is the intensity just perceptibly brighter than I, the initial velocity will be

$$(dx/dt)_{I+\Delta I} = k_1 (I+\Delta I) (a - x)^m - k_2 x^n, \tag{7}$$

no changes in concentration having yet taken place. Subtracting equation (4) from (7), we get

$$(dx/dt)_{\Delta I} = k_1 \Delta I \, (a - x)^m. \tag{8}$$

Assume that the just perceptible increment in intensity ΔI is recognized when $(dx/dt)_{\Delta I}$ is constant and equal to c'. This probably means that in a short time Δt, a constant increment of sensitive material Δx, must be decomposed by the addition of ΔI; this small increment Δx may show itself as a given increment in the frequency of impulses leaving the receptor cell to the associated nerve fiber (cf. Adrian and Matthews, 1927; Hartline, 1934). Equation (8) then gives $\Delta I = c'/k_1 \, (a - x)^m$. Dividing this value of ΔI by the value of I from equation (6) we get

$$\Delta I/I = c'/k_2 x^n \tag{9}$$

as a description of $\Delta I/I$ in terms of the general photoreceptor system. In other words intensity descrimination varies inversely as some power of the concentration of photoproducts present at the stationary state.

In order to compare this general derivation with specific data which give $\Delta I/I$ against I, it is necessary to replace x by I derived from the stationary state equations (5) and (6), and this requires specific values for m and n. When m and $n = 1$, that is, when both the primary light and dark reactions are monomolecular, equation (9) becomes

$$\Delta I/I = c \, (1 + 1/KI) \tag{10}$$

where $K = k_1/k_2$, and $c = c'/ak_2$. When $m = n = 2$, that is when both reactions are bimolecular, equation (9) becomes

$$\Delta I/I = c \, (1 + [1/KI]^{\frac{1}{2}})^2 \tag{11}$$

where $c = c'/a^2 k_2$. Equations (10) and (11) are shown graphically in figure 27; with them are the two curves expressing the situations when $m = 1, n = 2$, and $m = 2, n = 1$.

So far as the data of intensity discrimination are concerned only the symmetrical cases shown in equations (10) and (11) need be considered, because between them they describe all the measurements. Equation (10) is the curve which is drawn through the *Drosophila* data in figure 11. Equation (11) forms the curve for all the bee data in figure 12, for the data for *Mya* in figure 13, and for all the cone data of the human eye in figures 14, 15, 16 and 17. All these data are quite critical, and there is no difficulty in deciding which curves fit which set of measure-

ments. Smith's (1936) measurements of foveal intensity discrimina-
tion, made to test these ideas critically and perhaps antagonistically,
have been shown by him to correspond to equation (11) with extraordi-
nary precision.

For the rods of the human eye it is not possible to decide which equa-
tion applies because the data are too few; all four equations are equally
adequate.

c. *Visual acuity.* Measurements of visual acuity depend on the
recognition of a space between two contours. Because of the discrete
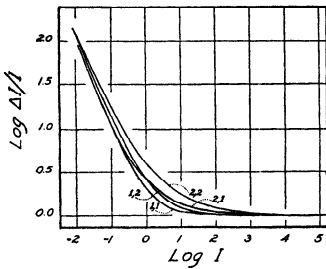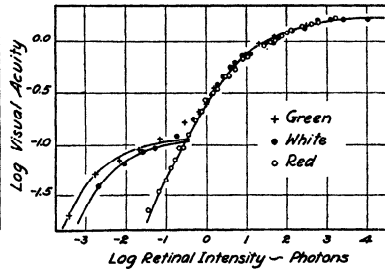

Fig. 27   Fig. 28

Fig. 27. The relation between $\Delta I/I$ and I in terms of the theoretical derivations.
Drawn on a logarithmic grid, the curves have a form which is independent of any
constants in the equations, but which is determined by the values of m and n
representing the order of the primary photochemical and dark reactions in the
photosensory system. The numbers attached to the curves show the value of m
and n in order.

Fig. 28. Relation between visual acuity and retinal brightness. The original
data are from Koenig (1897) and are shown in figure 25. For convenience, they
have been averaged in groups of five. The intensities have then been converted to
millilamberts, and multiplied by the corresponding average pupil area, using the
data of Reeves (1918), by the pupil efficiency factor from the data of Stiles and
Crawford (1933), and by $10/\pi$ to convert them into effective photons. The curve
through the cone portion of the data is the 2,2 curve (upside down) from figure 27,
while those through the low intensity rod portions are the 2,1 curve (upside down).

nature of the retina, this recognition requires the presence in the space
of one element, or of a given number of elements, which are stimulated
to a different extent than are the nearby elements which are covered by
the two contours. Visual acuity varies with intensity; therefore this
just recognizable space varies in size with intensity, from which it fol-
lows that the constant number of elements required for the recognition
of this space will occupy a variable area depending on the intensity.
This is a conceivable situation, and has indeed been described in con-
formity with the data in terms of certain ideas about the statistical

variation in threshold of the elements in the retinal population (Hecht, 1926, 1928).   This statistical treatment of visual acuity remains today much as when it was proposed; it describes the data quantitatively, and no other quantitative explanation has been proposed.   I have discussed this matter elsewhere (Hecht and Wald, 1933) and need not elaborate it here.

The whole problem of visual acuity and intensity may also be looked at from a different point of view, and I present it here because of its simplicity and suggestiveness.   Two lines are resolved as a doublet when the space between them appears of a different brightness than the lines themselves.   An object is seen as a C or an O depending on whether the circular image formed on the retina contains a break whose brightness is recognizably greater than the rest of the circle.   In other words, visual acuity may be intimately related to intensity discrimination, a suggestion first made in a rather general way by Helmholtz (1896) and later by Hartridge (1918) who studied it in detail for the special case of maximum retinal resolution.

Intensity discrimination varies with the prevailing intensity and so does visual acuity.   If the two functions are in some way related, they might bear the same relation to intensity.   Intensity discrimination is measured as the fraction $\Delta I/I$, and this fraction decreases as the intensity increases.   Visual acuity should therefore vary inversely as $\Delta I/I$, which means in terms of equation (9) that it should vary directly as some power of the concentration of photoproducts at the stationary state.   Putting visual acuity $V = bI/\Delta I$, and substituting in equation (9) we get

$$V = cx^n \tag{12}$$

where $c = bk_2/c'$ as a lumped constant.

The further solution of this equation in terms of specific values of m and n is exactly the same as for intensity discrimination.   In fact, the final curves plotted on a double logarithmic grid are identical with those in figure 27, but reversed in the sign of the ordinates.   Instead of going down, the curves go up in mirror image but have exactly the same forms.

Do visual acuity data fit these curves and equations?   It must be recalled that the equations apply to the retina, and that intensities at the retina correspond to outside intensities only when the pupil area is constant.   The measurements of intensity discrimination were made with constant pupil.   Koenig's measurements of visual acuity were unfortunately made with the natural pupil, as were most of the other

measurements discussed in section VII. I once (Hecht, 1928) cor-
rected Koenig's measurements in terms of the pupil data of Reeves
(1918). Since then Stiles and Crawford (1933) have shown that the
pupil is not efficient in transmitting light in proportion to its area, and
an additional efficiency factor must be added.

The original measurements of figure 25 have been averaged in groups
of 5, corrected for pupil area according to the average of Reeves, and
for pupil efficiency according to Stiles and Crawford, and are now all
put together in figure 28. Through their common, high intensity cone
portion the 2,2 curve of figure 27 has been drawn (upside down, of
course). It is the only one of the four curves which approximates the
data. The fit is not so good as one would like; and the reason for it, as
we know from measurements now being made in our laboratory by Dr.
Simon Shlaer, is that Koenig's cone measurements were not confined
to a single retinal location: the lower cone portion is parafoveal while
the upper is foveal. Shlaer finds that when the measurements are
deliberately confined to the fovea, the correspondence between the
data and the 2,2 equation is nearly perfect.

The rod portions of the white and green data definitely do not fit
either the 1,1 or the 1,2 curves. They do fit the 2,2 and the 2,1; the
data are not sufficiently critical for a choice. The curve drawn through
them is actually the 2,1 curve, for reasons which will become apparent
in a moment.

d. *Flicker*. Intermittent stimulation by light is interesting because
it makes an extra demand on the very simple receptor system suggested
at the beginning of this section. Intensity discrimination and visual
acuity have relied solely on the stationary state of the primary light
and dark reactions. Flicker involves in addition the secondary dark
reaction which follows them.

Under the influence of light, both primary reactions proceed, and the
velocity of their combined reaction is given by equation (4) derived
previously. In the absence of light, the primary dark reaction goes
alone, and the equation

$$- (dx/dt)_{\text{dark}} = k_2 x^n \tag{13}$$

gives the rate at which it forms the photosensitive material. In in-
termittent illumination these two reactions alternate rapidly, and form
a steady state in which what has been decomposed during the light pe-
riod is regenerated during the dark period. Since the light and dark
periods in all the measurements given in section VI are equal, the light

and dark velocities will be equal.   Putting equation (4) equal to (13) and solving, gives

$$KI/2 = x^n/(a - x)^m \qquad (14)$$

which, except for the number 2, is identical with the stationary state equation (5).   This is the basis for Talbot's law (Talbot, 1834; Hecht and Wolf, 1932; Arnold and Winsor, 1934).   The number 2 in the denominator depends on the equality of light and dark periods; the number to be used for any other ratio of periods is always the reciprocal of the fraction which the light duration is of the total light and dark cycle.

The effect of light on the photosensitive material is carried forward by the secondary dark reaction which the photoproducts undergo. According to equation (14) the concentration of these photo-products is x; therefore the rate of the secondary dark reaction is

$$(\Delta x/\Delta t) \text{ secondary } = k_3 x \qquad (15)$$

where k_3 is a velocity constant.   For the critical disappearance of flicker suppose that $\Delta x = c'$; that is, that the change Δx in concentration in the dark time Δt is just too small to cause the physiological change corresponding to a change in sensation of brightness.   As in intensity discrimination this may mean a change in discharge frequency of the cell (*cf.* Adrian and Matthews, 1927; Hartline, 1934).   The critical fusion frequency is f cycles of light and dark flashes per second; thus $f = 1/2\Delta t$. Substituting these values of Δx and of Δt in equation (15) we get

$$f = cx \qquad (16)$$

where $c = k_3/2c'$.   In other words, the critical fusion frequency is directly proportional to the concentration of photoproducts in the stationary state as given by equation (14).

The simplest four varieties of equation (14) are shown in figure 29. It is apparent that the value of n determines the slope of the steep limb of the curves, whereas that of m controls the curvature of the bend joining the steep limb with the horizontal one.

Examination of the data in figure 21 and in figure 23 shows that the rod curve always has twice the slope of the cone curve.   This determines the value of n in the two cases; $n = 1$ for the rods, and $n = 2$ for the cones.   The best curve to fit the cone data always has $m = 2$, and $n = 2$, as we just found also for intensity discrimination and for visual acuity.   The rods, however, are somewhat variable with regard to the

value of m. This is illustrated by figure 30 which contains the single measurements of two individuals (Hecht and Smith, 1936) with a 19° field and with white light. Besides showing the adequacy and reproducibility of the data, especially in relation to the theoretical curves, figure 30 indicates this systematic variability of the rod measurements. Of the six runs, the rod data of four are described adequately by equation (14) only when $m = 2$, while the two others are better fitted by $m = 1$. The rod measurements of Hecht and Verrijp (1933b) are also better fitted by far when $m = 1$. Figure 29 shows that when $m = 2$, $n = 1$, the curvature is more gradual; whereas when $m = 1$, $n = 1$,
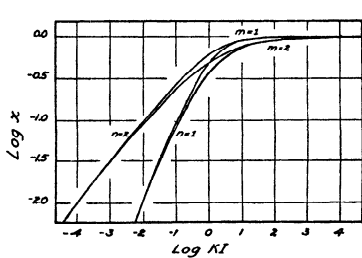

Fig. 29   Fig. 30

Fig. 29. The steady state equation (14) plotted when m and n are each 1 and 2. Because of the log plot the shape of the curves remains constant regardless of the values of K and a.
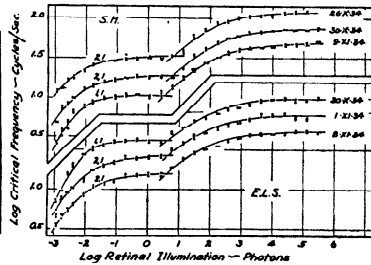
Fig. 30. The single, individual measurements of flicker as taken in the course of a run (Hecht and Smith, 1936). For convenience the separate runs (dated to the right) have been spaced 0.2 log unit apart on the vertical axis; the values on the ordinate scale refer only to the topmost run for each investigator. The numbers attached to the rod curves indicate the values of m and n in equation (14) used in drawing them. The curve through the cone portions of the data is always from $m = n = 2$.

the transition between the rising limb and the plateau is sharper. Also, the plateau itself continues to rise gently in the 2,1 curve, whereas it flattens off quite rapidly in the 1,1 curve.

Whether these differences really represent daily variations in the state of the rod photoreceptor system, it is hard to say. The consistency with which either one or the other type of curve appears is, however, impressive for us who have watched them for many months.

e. *Other functions.* It would be surprising if all the basic data of vision and photoreception could be described quantitatively in terms of so simple a system of ideas and equations as has been used for the three functions discussed in this section. It is true that the data of several

other properties have also been fitted by this mechanism (Hecht, 1934a). But most likely it will not be possible to fit all the data into such a simple system, because the reactions are certainly more involved than I have supposed.

The primary light reaction is probably simple enough, as many primary photochemical reactions are; but even with visual purple recent careful work shows complications, such as a dependence on pH (Chase, 1936), and a dark after-bleaching (Hosoya, 1933). The primary dark reaction probably also involves more than the direct reconversion of photoproducts into sensitive material, since Wald (1935b) has confirmed Kuehne's idea that visual purple may be formed from its products in two ways,—directly, and by the addition of new material,—and has shown (Wald and Clark, 1936) that dark adaptation brings these into evidence under certain conditions.

The important thing about the stationary state equation (5) is that, in spite of the simplicity of its derivation, it describes the relevant data with excellent precision, showing that fundamentally its simplicity is sound and that in the main its ideas are basic in the photoreceptor process. Naturally, complications are present. We hope soon to publish new measurements of dark adaptation (Hecht and Haig, 1936) which can be fitted theoretically only by a slightly more elaborate treatment. However, no matter what the complications are, the equations which describe them must reduce to the stationary state equation (5) since this equation describes the straightforward data of intensity discrimination, visual acuity, and flicker. Whatever else has to be added only serves to define more explicitly the nature of the photoreceptor process.

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