PROBLEMS OF PERIPHERAL VISION*

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THE RETINAL IMAGE

THE FIRST points to be considered in a study of peripheral vision are whether light can reach the periphery at all; and, if so, whether it suffers any loss of intensity as compared with the light reaching the fovea, and also whether the dioptric system is capable of producing a good image with the light which reaches the periphery. The reduction in intensity due to light-absorption in the media, which may be suffered by a ray of light striking the anterior pole of the lens, is roughly independent of the direction of passage when the pupil is not dilated. But the effective area of the pupil, acting as a stop in peripheral, as in foveal, vision, depends on obliquity. The first loss of intensity, however, occurs at the cornea. Does it vary appreciably with the perimetric angle?

FIG. 1 (a).—Section through anterior part of human eyeball, showing that the maximum angle of incidence of a visually effective ray of light on the cornea is about 70° from the perpendicular.

When a ray of light strikes the cornea, the finite size of even a dilated pupil limits the visually effective angle of incidence at the cornea to 70° (Fig. 1a). Larger angles can, of course, be formed by the ray and the visual axis; but, in order to be visually effective, the ray will have to enter at a point other than the corneal pole. Hence, it generally forms an angle of less

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than 70° with the perpendicular to the cornea. The bearing of this fact on the intensity of the ray transmitted by the cornea to peripheral regions is shown in Fig. 1 (b). To calculate the loss of intensity due to reflection at the corneal surface, the cornea was assumed to be a homogeneous, isotropic medium ($n=1.36$). An application of Fresnel's equations for various angles of incidence yielded the curve shown by the dotted line. At the limiting angle of incidence of 70° , a transmitted ray of light has lost only 15 per cent. of its intensity as compared with 2 per cent. at the normal angle of incidence. The curvature of the cornea reduces the value of 15 per cent., which applies either to a plane surface or an infinitely narrow beam. It follows that the corneal reflection factor hardly effects a difference in the intensity of light beams directed at the fovea or periphery, respectively.

FIG. 1 (b).—Angular variation of transmission.

The pupil is the first major structure affecting both the luminance and the shape of the retinal image. Using pupillo-

graphy, Spring and Stiles (1948) and Sloan (1950) accurately determined the relationship between the apparent pupil area A , and the obliquity of viewing it θ . A knowledge of this relationship is important because of its effect on visual threshold measurements in the periphery (*vide infra*). The principal component to vary is the horizontal pupil diameter d . This has often been assumed to provide a limiting factor to the extent of the temporal visual field f . Now the photographs in Spring and Stiles's paper give a finite value for d at 100° * and a slight extrapolation of their graph shows that d would not be zero even at 104° . This, however, is the value of f quoted by Hartridge (1952); Rønne (1915), on the other hand, gives a value of 107° . Since this value was obtained with a test field subtending at the eye an angle of 9° , the former value is more acceptable. Even so, a possible solution of the problem as to which factor determines the limit to the visual field is not to be looked for in an experiment in which the eye is illuminated externally.

From the point of view of vision, one wants to be certain that the whole

* All the angles refer to obliquities measured from the visual axis.

of the area as shown in Spring and Stiles's and also Sloan's photographs actually transmits light to the retina. Fincham (1954) suggested that trans-illumination of the sclera might help in this matter. It is found that, on trans-illuminating a fair person's sclera in the dark, the pupil glows with a characteristic red light, which disappears at a viewing angle of about 104° . But if faint illumination is provided externally along the subject's visual axis, the space between the distal side of the red glow and the coloured iris is found to be occupied at as small an angle as 45° by a black strip. This is presumably the inside edge of the iris. The effective pupil size, A , for peripheral vision is consequently smaller than pupillography would suggest. A precise re-determination of A , in which the external and internal pupillary edges are distinguished from each other, remains to be made if such visual functions as peripheral thresholds are to receive adequate interpretations.

The other functions of the pupil, namely its control of the distribution of light in the retinal diffraction pattern, and its effect on dioptric aberrations, also vary with the perimetric angle. To take the latter first: at about 70° , the horizontal diameter is so much narrower than the vertical that the difference affects the depth of focus of a measuring ophthalmoscope. As the eccentricity increases, the pupil becomes more and more slit-like; perhaps when we look out of the corners of our eyes, we obtain a glimpse of feline vision.

No one has ever seen a diffraction pattern on a human fundus, but there is little doubt that a point-source will give rise to the usual Airy disc (Fig. 2a) at or near the optic axis. The appearance of this pattern in the periphery is greatly complicated by refractive and other factors.

Nonetheless, the effect of the obliquity of the pupil can be isolated by means of a model (Weale, 1955a). When a circular aperture, with suitably bevelled edges, is rotated about a vertical axis, the circular pattern changes to an elliptic one (Fig. 2b). It is interesting to note that the size of the pattern is actually reduced as compared with the "normal". At a critical angle, which increases with the aperture of the lens system employed, the ellipses change to a system of hyperbolas (Fig. 2c). On further rotating the pupil—it has by now become slit-like—the pattern spreads horizontally (Fig. 2d) till a cut-off occurs.

FIG. 2.—Diffraction pattern due to a point source, and its variation with the angle of incidence on the aperture.

A similar variation of the diffraction pattern on the retina must be

envisaged. However, even if there were no complicating factors, the more dramatic changes would not occur except at great eccentricities, as a consideration of the aperture of the eye will show. These patterns will reduce only the precision with which an external object is imaged in the periphery. There visual acuity is so poor that it matters little whether a point source of light appears as a circular pattern, as a star, or as a streak. The spreading of the pattern, may, however, affect threshold measurements, a point to be considered below.

The effects of the properties of the lens on vision in the periphery can be subdivided into those which appear at relatively small perimetric angles, and others which appear only near the limit of the temporal visual field.

Ferree and Rand (1932) have shown on several eyes that a stigmatic image is produced on the retina only within a circle of angular radius 10° . Beyond this angle, even emmetropic eyes can exhibit marked irregularities, the most characteristic feature of which is a vertical positive astigmatism. The curvature of the eye-balls had a varied effect on these measurements, and no generalization is possible. Obviously one wonders whether refractive errors impede vision in the periphery to a measurable extent. Dobree and Weale (1954) measured the visual acuity at 55° and 70° , and found that the unpractised eye does not benefit much by a refractive correction. This result suggests that it is the retinal mosaic which limits the peripheral resolving power of the eye. Of the less important lenticular effects on peripheral vision, two will be mentioned. When the lens accommodates, the concomitant change in shape alters the shape of the over-lying iris, which leads to a slight increase of the visual field (Le Grand, 1946). In young dilated pupils, the anterior part of the lens actually protrudes through the pupil; this also leads to an increase of the field much as the curvature of the cornea enables us to see "round the corner". These effects are, however, counteracted in part by the angular variation of the reflection factor at the aqueous-lens surface (Fig. 1*b*, curve shown by a broken line). The greater the curvature of the lens, the smaller is the eccentricity at which light can strike the lens at a glancing angle and be transmitted to the retina.

A related phenomenon, namely internal reflection of light between the onion-like layers of the lens, renders any ophthalmoscopic examination of the extreme periphery impossible, and may further impede the imaging of objects in the periphery when the pupil is dilated, *e.g.* in the dark.

We are next faced with the question whether the retinal periphery can utilize the information which reaches it, or whether the visual acuity is so poor that the periphery can only signal the presence or absence of light.

The literature shows some confusion regarding the meaning of visual acuity. Thus Rønne (1915), whose work is still being hailed as "rarely surpassed in this sphere in its thoroughness", but of which it may more truly be said that "the modern touches here and there preserve it from the charge of nothingness", measured the perimetric angles at which stimuli of different sizes disappeared. He ignored the variation of light reaching the eye which

his method entailed, and his results (Fig. 3) can have only a limited application: an object subtending at the eye an angle of $27''$ was visible only at the fixation point. If this were generally true, Jessica's Lorenzo could never have called the star-lit sky "thick inlaid with patines of bright gold". Only one star or binary would be visible at any one moment. Rønne's claim to have measured a function of the visual acuity is largely based on the similarity between his results and those of Wertheim (1894). These still represent a classic of peripheral measurement and confirmatory work is not likely to find them seriously at fault. More recently, Mandelbaum and Sloan (1947) have measured visual acuity at various luminance levels. They covered the periphery up to an eccentricity of 30° . At a luminance level of $2 \times 10^{-2} \mu\text{L}$, the visual acuity was maximal at about 16° from the direction of fixation; at $0.4 \mu\text{L}$ the foveal centre could resolve only a grating as coarse as could be done at 30° . The shape of the curve relating visual acuity and eccentricity suggests that, at low luminance levels, visual acuity is mediated primarily by the rods.

FIG. 3.—Regional variation of visual acuity.

This finding, coupled with the observation of Aguilar and Stiles (1954)

that the rod mechanism is "saturated" at and above a luminance level of 200 ftL, throws some interesting light on the theoretical treatment of Wertheim's data by Doesschate, who assumed that peripheral visual acuity can perhaps be correlated with cone density, much as can be done with the resolving power of the fovea (*cf.* Ludvig, 1941). In order to test this view he plotted both Wertheim's data and the cone counts of Østerberg (1935) for different retinal locations on the same scale, and equated their respective maxima. The divergences between the two sets of data increases with the perimetric angle: visual acuity decreases more rapidly than does cone density. Doesschate (1946) suggests that this may well be expected, because the total number of cones in the retina, 7×10^6 (*cf.* Duke-Elder, 1938), feed their messages into nerve fibres only one-ninth as numerous. If the rods are also considered (7.5×10^7), it becomes clear that, in the periphery, many end organs are connected to a single fibre. Ten Doesschate concludes that the cerebral resolving power must depend on the number of fibres rather than on the number of cones, and a calculation based on the discrepancy between Wertheim's and Østerberg's data yields a number of retinal percipient units commensurate with the observed number of optic nerve fibres.

This agreement is impressive, but may be due, in part, to a coincidence. Wertheim does not state the luminance level at which he made his measurements, but the optical system he employed makes it unlikely that the level was above 200 ftL. Although the levels below this may be called "photopic", the rods participate in the visual process, and it is, therefore, uncertain to what extent the Østerberg curve used by Doesschate may have to be altered to allow for the number of active rods. In the second place, Wertheim's method of measuring visual acuity was "all-or-none", each of his points representing the mean of 24 observations; nonetheless, a statistical method would probably yield higher values, when the discrepancy between classical and statistical thresholds would increase with eccentricity. Only when the so-called "mesopic" luminance state, in which both rods and cones are stimulated, has been fully investigated will a clearer answer to the problem raised by Ten Doesschate be obtainable.

SENSITIVITY

The term sensitivity will be deemed to have its orthodox meaning, namely, the reciprocal of that light energy for which the visual response is a constant, other factors being varied. This emphasis is necessary because in several papers published since 1945 the spectral variation of any one visual phenomenon faintly reminiscent of some standard sensitivity curve has been identified with it, although no energy measurement has been made.

(a) *The Dark-Adapted Eye*.—The best-known visual property of the dark-adapted retinal periphery is its considerable sensitivity to light; it is about a thousand times more sensitive than the dark-adapted fovea (Hecht, Haig, and Wald, 1935). Arden and Weale (1954) have shown that this factor is due

to differences, not so much in the concentrations of light-sensitive pigments in the rods and cones as is commonly assumed (Wald, 1954), but in the respective summing ability of foveal and extra-foveal regions. The curves in Section C of Fig. 4 (opposite) represent orthodox dark-adaptation curves as measured extrafoveally (8°) with a white test-field subtending at the eye an angle of 7° .

When similar measurements were made with a minute test-field, the curves in Section A were obtained. The results when the small field measurements were repeated in the central fovea, are shown by the curves in Section B.

Two points of interest emerge:

(i) The later branches in A and C, usually associated with an increase in rod-sensitivity in general and re-accumulation of the bleached visual pigment in particular, cannot be superimposed. But the reverse would be expected to be the case, if the phenomenon were due only to photo-chemical changes. Arden and Weale explain their finding by postulating an increase in the size of the receptive field during dark-adaptation.

(ii) The second and more surprising point is that after about 20 minutes, the curves in Sections A and B, measured for the para-fovea and central fovea respectively, show approximately equal sensitivities. This finding confirms others pointing in the same direction (Stiles and Crawford, 1937; Craik and Vernon, 1941; Baumgardt, 1949), and suggests that the hypothetical difference between the visual pigment concentrations in the rods and cones cannot be the only factor responsible for the difference observed when foveal and peripheral thresholds are measured with large fields (Weale, 1955b).

The enhanced summing power of extra-foveal regions helps to ensure that the image of even a minute source of light, diffused over a bigger area owing to the physical factors enumerated above, may elicit a visual response.

When the sensitivity of the dark-adapted eye was measured at various perimetric angles with white light, the results shown in Fig. 5B (overleaf) were obtained (after Stiles and Crawford, 1937). These data refer to a nearly horizontal meridian in the temporal visual field, so chosen as to avoid the blind spot. A belt of high sensitivity surrounds the fovea and rises to a maximum at about 15° from the fixation area. Doesschate (1949) has shown that the regional variation of the absolute threshold correlates fairly well with the rod distribution as found by Østerberg (1935). The correlation is not perfect (Fig. 5A, B), even though allowance has been made for the effective pupil area, but it is good enough to carry conviction. A similar result was obtained by Sloan (1950). These data lead to the conclusion that the regional variation of the absolute sensitivity of the dark-adapted human eye is fully accounted for by the regional variation in the rod density; there is, therefore, no need to assume a regional variation in the density of the rod visual pigment.

This view has recently been confirmed by the work of Campbell and Rushton (1955) in which relative density changes due to the bleaching of a living human eye were determined at various perimetric angles. Although

FIG. 4.—Dark-adaptation curves. (By courtesy of the editors of the *Journal of Physiology*.)

the recovery curve of the bleached pigment shown by the authors is bipartite (the possible contribution to the overall bleaching made by extra-foveal cones being ignored), it is certain that the bleaching of mainly visual purple is responsible for the observed effect. Campbell and Rushton's results (Fig. 5A) shows unequivocally that there is a close topographical parallel between rod population, absolute thresholds, and changes in pigment density.

FIG. 5 (A).—Correlation between regional variation of rod density (full line) and relative pigment density (dots).

(By courtesy of Campbell and Rushton (1955) and the editors of the *Journal of Physiology*.)

FIG. 5 (B).—Regional variation of sensitivity of the dark-adapted eye (two observers).

(b) *The Light-Adapted Eye*.—As the level of adaptation of the eye is raised the threshold increases (Crawford, 1947) till, at relatively high luminance levels, the fovea becomes more sensitive than the periphery. The reversal of the relative positions of these retinal parts on the sensitivity scale is usually explained by postulating the cessation of rod-activity at photopic luminance levels. The superior foveal sensitivity might thus be due either to a greater cone density or to a greater cone-pigment density: the foveal cones are about three times as long as those in the periphery (Polyak, 1941), a factor which might partly account for the observed difference (*vide infra*).

Now Aguilar and Stiles (1954) have shown on four experienced observers (Fig. 6, overleaf) that the rods contribute to the visual process at levels usually called "photopic". The upper luminance arresting their activity is

at 200 ftL, the retinal region under test being 8° from the fovea. Oikawa and Kurosawa (1954a, b) put it at about 1 ftL in the same retinal region, but at about 20 ftL when the eccentricity is 50° . Again, according to Sloan (1950), rod and cone thresholds are approximately equal at 1 ftL. It is, therefore, doubtful whether the more rapidly decreasing sensitivity of the peripheral regions, as due to light-adaptation, can be ascribed primarily to a failure in the rod-mechanism, rather than to its saturation.

The regional variation of the sensitivity of the light-adapted eye does not seem to have been measured. An estimate of this function can, however, be made by using Weale's spectral sensitivity data (1951b; 1953a). The

values of $\frac{1}{m-n} \sum_{\lambda_m}^{\lambda_n} S_\lambda$, the mean sensitivity for an equal-energy stimulus, are

plotted for various perimetric angles in Fig. 5(c). Data were obtained at two luminance levels, the relative positioning of foveal and peripheral curves being established by brightness matches between foveal and peripheral

FIG. 5(c).—Correlation between regional variation of cone density and sensitivity of the light-adapted eye.

FIG. 6.—Mean results for four subjects showing variation in increment threshold with field intensity. The ordinate values of Curves A, B, and C have been displaced to facilitate comparison. Curve D is in its correct position. Section (c) indicates field range of rod-saturation; Section (d) is probably due to intervention of cone-mechanisms.

(By courtesy of Aguilar and Stiles (1954) and the editors of *Optica Acta*.)

stimuli ($\lambda = 589 \text{ m}\mu$). The average of the data of Stiles and Crawford (1933a), measured at an even higher luminance level at 0° and 5° , is also shown. No significant change results from plotting the data for an equal-quantum spectrum. All three curves are corrected at 0° for light absorption by the macular filter (Wald, 1949). No correction for the effective pupillary diameter was applied to Weale's data, since his optical system involved focusing a narrow slit-image in the plane of the observer's pupil, and the beam was thus not cut off. Since the retinal direction effect (Stiles and Crawford, 1933b) is negligible in extra-foveal regions, no correction need be applied for the precise point of focus in the observer's pupil. It is possible to make a comparison similar to Doesschate's but using Østerberg's cone counts (Fig. 5c). When corrections are applied for differences in the counts as between the nasal and temporal retina respectively and also for the types of test-field employed, an approximate correlation is obtained between the data for a luminance level of 70 ftL and the cone-density in various regional parts. The discrepancy occurring at 10 – 15° may be ascribed to the contribution to vision still made by the rods; Fig. 5(A) shows that they are particularly numerous in this region. Since the aforementioned difference between the foveal and extra-foveal cone dimensions is inadequate to account for the observed regional variation in sensitivity, greater weight may be given to the variation in cone density.

As with the rods, the correlation suggests that the concentration of cone pigments does not vary much across the retina. But such an argument should not be pressed, since no account has been taken of the different types of cone or pigment demanded by explanations of the various phenomena of colour vision. A confirmation and extension of the above results to higher luminance levels and more perimetric angles is certainly desirable.

(c) *Spectral Sensitivity Curves*.—The work of various authors published during the last 20 years suggests that the light-adaptation of the fovea has a measurable effect on the shape of the foveal spectral sensitivity curve. Thus, when there is a zero surround (*cf.* Wright, 1946; Wald, 1945; Thomson, 1951), the curve tends to be relatively lower at short wavelengths than when there is a white background or surround (Stiles and Crawford, 1933a; Weale, 1951b; but see also Stiles, 1946; Hurvich and Jameson, 1953). That chromatic adaptation (Jameson and Hurvich, 1953) should produce a difference is not surprising, but these foveal effects are dwarfed by the effects of adaptation to a surround on extra-foveal spectral sensitivity curves. The situation is much more complicated than would appear on the basis of the classical theory of duplicity.

If due allowance be made for pre-retinal absorption, the sensitivity of the fully dark-adapted eye to a spectrum of equal quantum intensity is greatest at about 500 $m\mu$ and can be fully accounted for in terms of visual pigment 497 (visual purple, *cf.* Crescitelli and Dartnall, 1953). What of the periphery which is not dark-adapted? Walters and Wright (1943), measuring the spectral sensitivity curve at an eccentricity of 10° for a number of luminance levels (of the test-field) with zero surround, found that the spectral sensitivity maximum moved from about 500 $m\mu$ at the lowest level to 540 $m\mu$ at the highest. It was impossible to obtain a curve agreeing with the foveal one (max. 555 $m\mu$). The usual energy limitations at the short wavelength end of the spectrum restricted their measurements to wavelengths longer than 480 $m\mu$.

The curve obtained by Wald (1945) at 6° from the fovea is in substantial agreement with the data of Walters and Wright.

The first intimation that light-adaptation of large extra-foveal regions can provide information about retinal activity other than that gained from foveal and "scotopic" peripheral spectral sensitivity curves was given by Stiles and Crawford (1933a). These authors, examining both the central fovea and an extra-foveal region at 5° at a level of adaptation of 300 c/sq.m (white surround), made three interesting observations:

- (i) Both the foveal and the extra-foveal curves were tripartite, showing humps and shoulders in the violet, green, and orange ranges of the spectrum;
- (ii) The "violet" hump was relatively more pronounced in the extra-foveal curves;
- (iii) The extra-foveal visibility was generally lower than the foveal.

Recent work has confirmed the suggestion of Stiles (1949) that adaptation to white light has a less marked effect on the short wavelength mechanism characterized by the "violet" hump, than on the others contributing to the spectral sensitivity of the light-adapted eye. For a reason still awaiting elucidation, this applies with greater force to the periphery than to the fovea.

The work of Stiles and Crawford has been extended by the present writer (Weale, 1951b, 1953a) to an eccentricity of 70° . This seems to confirm the view that white light depresses the sensitivity of the eye to light of long wavelengths more than the sensitivity to short wavelength radiations. The light-adapted periphery was also shown to be relatively much more sensitive to light of short wavelengths than is the fovea. These findings have recently been confirmed by Auerbach and Wald (1954) and by Moreland (1955). Wald (1951) previously measured foveal and extra-foveal "cone" sensitivities at ten wavelengths evenly distributed between 360 and 750 $m\mu$, and the observed difference between the two sets of data was ascribed to the absence of macular pigment from the extra-foveal position at 6° . Now Weale (1953a) observed that, when the retinal periphery is stimulated with blue light which is surrounded by a white field and the latter is suddenly extinguished, the sensation due to the blue light begins to fade at once. Other spectral regions did not produce this effect. This suggests that the short wavelength mechanism rapidly adapts. Auerbach and Wald (1954), measuring the rate of dark-adaptation of the strongly light-adapted periphery (5×10^5 mL at 6°), found a more rapid initial rate of dark-adaptation at $\lambda = 436 m\mu$ than at any other of the wavelengths tested. The spectral sensitivity curve given by these authors for an eye which has been dark-adapting for one minute is greatest at 436 $m\mu$. Since they could obtain an almost orthodox "cone" curve by pre-adapting the eye to blue light, they conclude that the maximum at 436 $m\mu$ must be due to a "violet" cone. The light-absorption by the macular pigment is thus only partly responsible for the difference between foveal and extra-foveal curves.

Although thorough light-adaptation has brought to light facts about peripheral sensitivity mechanisms which the propounders of the duplicity theory could hardly have envisaged, these are, from a theoretical point of view, a mixed blessing. Consider the case of a surround. To what extent is its effect due to nervous influence of one retinal region on another, or the action of scattered light? Le Grand (1937) has shown that, at close range, the latter effect predominates over the former, but at large distances from a retinal image it is easier to account for the effects he observed by postulating trans-retinal neural activity. Since surrounds are usually so arranged as to be close to the test-stimulus (*cf.* Lythgoe, 1940), the physical effect would at first sight be expected to operate. If this be so, why do many authors emphasize the fact that their adapting surrounds or fields are large? This surely suggests that it is the adapting parts more remote from the test-field which produce the phenomena observed under conditions of thorough light-adaptation. Nonetheless, the more proximate parts will affect the picture,

if only by veiling glare sources. Indeed, this factor is considered to play an important role in spectral sensitivity curves, measured electro-retinographically, and will be referred to again in a later section. Meanwhile, it is well-nigh impossible to account for the peripheral spectral sensitivity curves in physical terms. There is no doubt that scattered light will lower the absolute sensitivity, as will any other large and intense glare source. Now, if Rayleigh scattering takes place in the ocular media, an originally "white" adapting light will be somewhat denuded of short wavelength radiation, and thus tend to depress the sensitivity of long wavelength mechanisms much as yellow or orange light would. The short wavelength mechanisms would be left relatively undisturbed. That this cannot be the complete explanation is shown by the vast difference between the effects of such an adapting light on foveal and on peripheral vision. Furthermore, peripheral wavelength discrimination is found to vary with luminance (Weale, 1951a, 1953a), another factor which suggests that light-adaptation produces functional changes in the relative efficiencies of the retinal mechanisms.

Summarizing, it would appear that there are at least three types of spectral sensitivity curve which characterize the retinal periphery.

When it is fully dark-adapted, the sensitivity is maximal at 497 $m\mu$ and hence almost certainly mediated by visual purple. When the light-adaptation of the periphery is only local, as happens with a bright test-field and zero surround, the spectral sensitivity curve is similar in shape to the foveal curve but is so displaced that the maximum moves from 555 to 540 $m\mu$. When the level of adaptation of a large part of the retina is raised to a high luminance,

the spectral sensitivity curve becomes bi- or tri-partite, and its maximum is eventually located in the short wavelength region of the spectrum.

(d) *Glare*.—Petherbridge and Hopkinson (1950) have recently obtained data which show the variation of surround luminance, B , with the perimetric position of a glare source ($>3^\circ$) when the "degree of glare" is kept constant. It is at once apparent that these data (Fig. 7) cannot be readily

FIG. 7.—Decrease of effect of glare source with eccentricity.
(By courtesy of Petherbridge and Hopkinson (1950) and the editors of the *Transactions of the Illuminating Engineering Society*.)

interpreted in terms of retinal function, since the variation of B necessarily involves a change in the level of adaptation of the eye as a whole. But the data shown, *e.g.* in Fig. 5(B), refer to fixed levels of adaptation. This distinction serves to emphasize a possible physiological aspect of glare. A source of light will be a potential glare source only if it sets up a local adaptational effect different from that due to the general level of adaptation. Thus a 150w lamp, when viewed directly at night, may give rise to discomfort glare. When we view the same lamp on the following day against a bright sky seen through a window, we may hardly realize that the light is switched on.

But, as Weston (1953) has emphasized, a marked psychological element enters the whole problem. On an unlit road, the appearance of one or two glare-sources in the peripheral field may cause acute discomfort if we resist the impulse to fixate and disaster if we yield to it. This raises another interesting point in connection with Petherbridge and Hopkinson's data.

When laboratory experiments or practical visual tasks are performed in the presence of an extra-foveal glare source, the impulse to fixate the latter must be resisted. Fig. 7 shows that, up to an eccentricity of about 30° , the glare effect is fairly uniform and drops sharply at eccentricities greater than this. In the absence of any experimental evidence, we have to consider the possibility that the fixation reflex is approximately equally effective up to about 30° , but that it suffers from an attitude of *laissez-faire* beyond this angle. On this basis, peripheral glare would have a nervous component which might be separable from an intensity factor by a special experimental procedure, perhaps on the lines suggested by Gerathewohl (1951).

COLOUR VISION

Not very much remains to be done on the "scotopic" visibility curve, since it can be adequately accounted for in terms of pre-retinal absorption, light quanta, and the absorption characteristics of visual pigment 497. There is, of course, a well-known gap in our knowledge—namely what happens between the rods and consciousness—but this is not specific to the problem. No corresponding progress has yet been made with the photopic visibility curve or the fundamental response curves, and in some way or other, most efforts aim at a release of visual theory from this impasse. Peripheral investigations can make a contribution and, as we have seen, have already done so. Entirely new methods are now being brought to bear on the problem. Unlike the classical method of investigation—that of chromatic sensations—they depend on the electrical properties of the stimulated eye, and have yielded information primarily about the retinal periphery.

(a) *The Method of Chromatic Sensations.*—The older workers, whose interest in peripheral colour vision was prompted by the desire to support some theory or other, restricted their attention to the appearance of coloured lights or pigments (*cf.* Weale, 1953b). They normally employed a perimeter

and the observer had to signal at which perimetric angle a chromatic sensation became achromatic or *vice versa*. Today, even modern experiments along such lines are regarded by many with indifference, because, it is argued, the description of sensations is controlled by so many imponderable factors. The broad results of such perimetric measurements are these:

- (1) "Blue" is recognized farther in the periphery than any other colour, "red" has the smallest perimeter, "yellow" and "green" occupy intermediate positions (Abney, 1913);
- (2) When no restriction is placed on luminance the colour-fields for a 1° field are co-extensive (Wentworth, 1930);
- (3) Adaptation has a profound effect on the extent of the fields (Wentworth, 1930);
- (4) There are certain invariant chromatic sensations (Hess, 1889) when various perimetric angles are examined. This invariance does not extend to the purity of the "constant" colour, but in general reds and greens are said to tend towards yellow, and blue-greens and violets towards blue.

Attempts at a quantitative appraisal of colour vision in the periphery are very recent. In this connexion, it is useful to distinguish between the influence of peripheral areas on foveal colour-vision on the one hand, and the colour-vision of isolated peripheral parts on the other. Wright (1946) has shown that pre-adapting the central retina to a white field (5°) reduces the just noticeable wavelength step ($\Delta\lambda$), when $\lambda=530$ and $580\text{ m}\mu$, but increases it for $\lambda=494\text{ m}\mu$. It is uncertain whether similar effects would be observed by pre-adapting the fovea with a white field of only 2° or whether a stimulation of the parafovea is essential.

Hunt (1952) used a binocular matching method in which a bi-partite 20° test field was surrounded by an adapting field of 60° . The adapting illuminant was S_B . Trichromatic matches were made of eight coloured lights in turn; it was found that when the eye was adapted to low luminance levels an increase in the intensity of the test colour led to an increase in colour saturation. A corresponding increase in the intensity of the test colour when the eye was adapted to high luminance levels led to most colours appearing bluer. A broadly similar result was obtained when the test field subtended an angle of only 1° (Hunt, 1953). Although care must be exercised in deducing the subjective appearance of stimuli from the shape of sensitivity curves, Hunt's results for high levels of luminance are compatible with the view that white light tends to depress the response to long wavelength light more than that to light of short wavelengths.

Burnham (1951) examined the effect of field size on chromaticity. An increase of from 2° to 22° led to a small but significant increase in saturation. A further increase of the area to 77° produced only smaller and non-systematic changes. The stimuli in these experiments were necessarily unsaturated and it is of some theoretical interest to know whether spectral stimuli would behave in a similar manner.

It follows from Hunt's and Burnham's work that, under given conditions,

the stimulation of the extra-foveal regions improves the chromatic perception of the fovea. Neither author reports any regional variation of the resultant sensation.

The colour vision of isolated peripheral regions has lately received some attention both in Germany and in Great Britain. Thus Baeuml and Engelhardt (1951) and Engelhardt (1951, 1952a, 1952b) have observed peripheral colour sensations, the stimuli being provided by Ostwald papers. According to these experiments, the periphery is trichromatic or anomalously trichromatic up to an angle of about 45° , and dichromatic beyond this. The extreme periphery is said to be achromatic. The authors' use of these well-defined terms is open to criticism, as no colour-matching experiments were carried out (but *cf.* Moreland, 1955).

Since, moreover, the perimetric fields are a function of the intensity and field size of the stimulus and the level of adaptation (Abney, 1913; Wentworth, 1930), the validity and value of such a generalization are questionable.

Some workers believe that monochromatic stimuli are preferable to coloured papers, if only for the reason that they simplify comparison and correlation with kindred work. Gilbert (1950) measured the just noticeable wavelength step ($\Delta\lambda$) at an eccentricity of 4° at two luminance levels, and observed that desaturation occurred at the lower level in the blue-green region of the spectrum. She ascribed this to rod activity. Weale (1951a) extended this work to 70° and observed a gross deterioration of wavelength discrimination at long wavelengths as the perimetric angle increased. Rather unexpectedly, the values of $\Delta\lambda$ at short wavelengths suffered comparatively little.

The most comprehensive investigation of the chromatic properties of the retinal periphery, however, was made by Moreland (1955), who modified the Wright colorimeter to enable him to reach perimetric angles as large as 45° and determined colour-mixture functions at various eccentricities. He found that, in the absence of a surround, vision was trichromatic up to 15° , dichromatic between 15 and 25° , and nearly monochromatic at 40 – 50° . He confirmed the observation mentioned earlier that the periphery is very susceptible to the effects of different levels of adaptation, and discovered that the technique, measurement, and length of exposure of the eye to the test field all play important roles. His results on the colour changes observed when the test field moves away from the fovea contradict Hess's discovery of invariant colours: Moreland did not find any stimuli which produced them. His data on spectral sensitivity and wavelength discrimination agree with the findings of Stiles and Crawford and of Weale. His results on spectral sensitivity raise an interesting point requiring further elucidation: the curves are humped even in retinal regions where colour-matching data suggest that vision is monochromatic. Since such humps (*cf.* Stiles, 1949; Weale, 1953c) are probably caused by the selective sensitivity of retinal colour mechanisms, we are faced with the interesting situation in which the mechanisms are clearly in action but the wavelength discrimination is nil.

(b) *The Method of Electrical Phosphenes.*—This technique was developed by Motokawa (1949a). Briefly, two silver electrodes are secured to the human skin with electrode paste, one above the eyebrow and one to the homolateral temple. The electrodes are connected through a switch and a variable resistance (10–10000 Ω) to a 12-volt battery. Electrical stimulation of the eye is achieved by passing a current through the circuit for 100 m.sec. An adequate stimulus elicits in the observer a phosphene. The threshold strength of the phosphene depends on whether or not the eye has been exposed to light. The electrical excitability of the human eye recovers rapidly after a brief exposure and then becomes supernormal. When the eye is exposed for one or two seconds or less to white light and the electrical excitability measured during the following few seconds, the resultant curve is found to exhibit three maxima when the light stimulation is foveal. The maxima are subsequently shown to be associated with mechanisms responding primarily to red light (1 sec.), green light (2 sec.), and blue light (3 sec.). These temporal points are independent of the intensity of the light stimulus (Fig. 8a).

FIG. 8 (a).—Excitability curves, produced by red (R), green (G), and blue (B) stimuli. Black and white symbols refer to two different measurements.

An important feature of this method is the phenomenon of multiple thresholds. Let us suppose that the pre-illumination is green and a relatively high voltage is applied. The observer is going to signal: phosphene. As the voltage is reduced, the phosphene disappears, but further reduction of the voltage allows the phosphene to reappear; the voltage is reduced even further and the phosphene disappears again; further reduction can yield a third threshold (Motokawa, 1951). These various thresholds are associated with different spectral mechanisms; it is like going down a mine near an incline when various strata, seen on the Earth's surface, reappear in turn. When Motokawa (1949b) came to examine the periphery of an observer with normal colour vision, the excitability curve showed a new maximum of

1.5 sec. after cessation of white stimulation. The spectral variation of this mechanism is maximal at $585\text{ m}\mu$ and dominates the retinal region at 15° . At 25° the "blue" mechanism takes the lead, which it keeps at 35° (Fig. 8*b*). In the outer regions this method fails to distinguish between the "green" and rod mechanisms (but *vide infra*). It might be argued that this result has dealt a death blow to the trichromatic theory, but this is not the case since no one knows which retinal structure gives rise to the phosphene. As Thomson (1952) has pointed out, the phosphene records probably refer to an intermediate zone, and moreover the spectral curves do not represent energy relations. The old heresy of identifying bell-shaped spectral variation curves with each other might, in the present case, lead to unnecessary complications. Motowaka's technique has been most fruitful and led to a large amount of work from his school. Oikawa and Kurosawa (1954*a*), measured the response of the rods by determining the phosphene threshold when the eye was pre-illuminated with lights of various wavelengths obtained from an equal-energy spectrum. Six retinal areas of eccentricities ranging from 5° to 50° were examined at three intensity levels. Only the curves at 40° and 50° were smooth; in the other retinal regions the high intensity curves showed marked indentations at 530, 575, and $670\text{ m}\mu$. The authors ascribe them to inhibitory activity of the cones responding mainly to lights of these wavelengths.

Oikawa and Kurosawa (1954*b*) also observed the behaviour of rods in photopic vision (*vide supra*); examining a retinal region at an eccentricity of 20° , they found that a white flash (40 m.sec) led to the following results:

- At 300 lux the excitability curve showed the "red", "yellow", "green", and "blue" peaks;
- At 50 lux the "yellow" and "blue" peaks appeared, which persisted down to the light threshold;
- At 10 lux the rod peak appeared (4.5 sec. after cessation of the white stimulus), and this also persisted down to the light threshold;

FIG. 8 (*b*).—Spectral variation of excitabilities at various retinal locations.

(By courtesy of Motokawa (1949*a, b*) and the editors of the *Tohoku Journal of Experimental Medicine* and the *Journal of Neurophysiology*.)

When the luminance was 50 lux and different retinal regions were compared, four peaks appeared at 5°, only "yellow" and "blue" at 20°, but "yellow", "blue", and "red" at 50° in the periphery.

These results are striking, but the reader will indubitably have noticed that, in the former work, there was apparently no inhibitory activity in the blue part of the spectrum. Oikawa and Kurosawa write:

If the blue receptor is so much akin to the rod as Roaf [1933] and recently Willmer [1943] emphasize, we shall be able to understand the reason why the blue part of the spectrum has no such inhibitory action upon the rod-response as do red, yellow, and green parts of the spectrum."

In the second paper, however, "red" and "yellow" as well as "blue" peaks appeared in the excitability curve. Oikawa and Kurosawa write:

If the theory by Roaf and by Willmer were correct, it would be difficult to understand the fact that in our experiment the rod process and the blue process can be distinguished very clearly from each other. As was shown in a previous [*i.e.* the above] paper, the rod process shows a spectral distribution well corresponding to the scotopic visibility curve, and never shows a sensitivity maximum at the blue part of the spectrum under all experimental conditions.

The difficulty of reconciling these two conclusions may be linguistic in nature but has every appearance of being logical. The aforementioned agreement with the scotopic spectral sensitivity curve is only achieved after an arbitrary arithmetical manipulation which the reader can only partly justify if he happens to have read another paper by Oikawa (1953).

Such obstacles induce the belief that the writers of the Japanese school have yet to map the land over which they have been promising to guide us.

(c) *Electroretinography*.—The only objective method so far suitable for investigation of colour mechanisms in the human eye is provided by the electroretinogram (ERG). The electrical response of the eye giving rise to the various components of the ERG is relatively so poor that either intense or extended stimuli are required to obtain any information at all. This means that by far the larger retinal part examined is extrafoveal.

The three components of the human ERG which lend themselves to quantitative analysis are the *a*-, *b*-, and *x*-waves (Fig. 9, overleaf). The positive *x*-wave was discovered in man by Motokawa and Mita (1942) and Adrian (1945). Although Best (1953) rightly insists that great care is to be exerted in associating any ERG component with a particular retinal structure, there is little doubt that the *x*-wave is due to a cone response. Thus Adrian observed it in the light-adapted eye with red but not with blue light. The latter favoured the appearance of the positive *b*-wave. He also showed that animals whose retinæ contained many cones yielded ERGs with both *x*- and *b*-waves, but that those with few cones gave only *b*-waves. Schubert and Bornschein (1952) have shown that the *x*-wave is absent in [rod] monochromats and, above all, in protanopes. To date, it does not seem to have been possible

to construct a spectral sensitivity curve of the *x*-wave, although this has been achieved with *a*- and *b*-waves.

These data (Riggs, Berry, and Wayner, 1949; Armington, Johnson, and Riggs, 1952) were obtained with a $7^{\circ} 30''$ field and thus covered a large extra-foveal region. Now, although Adrian (1945) had observed that the negative *a*-wave appeared in the human eye only at high intensities, Armington and others (1952) found that its spectral distribution was similar to that of the *b*-wave, both being comparable with the scotopic visibility curve; they write:

One conclusion which seems inescapable is that the *a*-wave, as grossly observed, is not a purely photopic effect.

Although comparable with the scotopic visibility function, these data can in no way be identified with it: their maximum is displaced by about $20 \text{ m}\mu$ towards the short wavelength end of the spectrum. Boynton (1953) has investigated the suggestion that this hypersensitivity to short wavelength radiations might be due to light scattered by the ocular media. According to this view a large test field would "waste" less light than a small one. Boynton thus measured the spectral sensitivity of the *b*-wave with fields of diameter between 12° and 105° , and found that the large fields in fact gave lower sensitivity values to blue light than the small ones. After the application of a correction based on the assumption that the scattering is of the Rayleigh type, the two curves agree with each other at short wavelengths but their previous agreement at longer wavelengths is destroyed. Boynton ascribes this disagreement to the neglect of a correction factor due to the reflection at the red fundus. To meet the discrepancy, this correction would imply that the fundus reflects about 100 per cent. of the incident orange light. In any case, this correction would have to be applied to both the large and small field data and thus a comparison between the two cannot reveal the necessity for its application. The verdict on the effect of stray light on spectral ERG curves is thus "not proven". A possible explanation of the discrepancy discovered by Boynton might be provided by the measurement

FIG. 9.—Electoretinograms (Up = positive; Down = negative). A and B: colour-normal eye; C and D: protanopic eye.

A and C stimulus containing light of wavelengths $> 530 \text{ m}\mu$; B and D stimulus containing light of wavelengths $> 600 \text{ m}\mu$.

Note that D lacks first positive inflexion (*x*-wave).

(By courtesy of Schubert and Bornschein (1952) and the editors of *Ophthalmologica*, Basel.)

of spectral *b*-wave sensitivity curves at various luminance levels, or by chromatic adaptation experiments.

Such have recently been undertaken by Armington and Thiede (1954), who have succeeded in separating several independent spectral processes. More recently, Armington (1955) published results of spectral sensitivity measurements in which the ERG had been elicited with stimuli subtending at the eye angles of 6°, 30°, and 60° respectively. The fields were fixed centrally and Armington concluded from the shape of the three curves—broadly similar for the three field sizes—that they were intermediate between pure foveal curves (Hsia and Graham, 1952), and pure peripheral curves (Weale, 1953a). He also argued from his results that the role of scatter is inappreciable in photopic ERG measurements, but he failed to come to grips with the question of macular pigmentation. A similar failure vitiates Johnson and Cornsweet's conclusions (1954), drawn from a comparison between the CIE photopic curve (2° field) and an ERG sensitivity curve obtained with a 7° 30' field. In this connexion, it is most important to observe the stipulation made by Armington (1955), namely that only comparable data should be compared.

These results are still too imprecise to justify a detailed comparison with data obtained by other methods, but human electroretinography may well catch up with the results obtained from subjective work and allow further investigations into the processes of colour vision.

CONCLUSION

Aspects of the function of the retinal periphery ranging from diffraction phenomena to electrophysiology have been discussed.

Other important subjects, such as reaction times and fusion frequencies, have been omitted, but those dealt with have shown that peripheral vision is a difficult subject to study. To take a pleasant task, namely the leisured contemplation of paintings, the retinal periphery provides a most acceptable *éminence grise*; Van Gogh's "Potato-eaters" would look toneless with a light surround, Constable's landscapes simply like views through a window if the background were dark. It would appear that some consideration of the properties of the retinal periphery may lead to increased visual hygiene, if not also to greater visual efficiency.

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