The directional sensitivity of the retina and the spectral sensitivities of the rods and cones

BY W. S. STILES, The National Physical Laboratory

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1. Introduction

It is now well established that light rays of the same spectral character and physical intensity entering the eye through different points of the pupil may produce visual impressions which differ in brightness and colour even though the patch of retina stimulated (the fovea) is kept the same.* Rays entering the eye through different points of the pupil and terminating on the same point of the retina are incident on the retina in different directions. Also, they have traversed different paths in the refractive media of the eye and may have suffered different losses by absorption, scattering or reflexion. It has been shown, however, that differences in the light losses in the refractive media do not account for the observed variations in visual response, which must therefore be attributed to variations in the reaction of the retina to light incident on it in different directions or, briefly, to a

* See Stiles and Crawford (1933), Dziobek (1934), Wright and Nelson (1934), Goodeve (1936), Stiles (1937) and Crawford (1937).
The directional sensitivity of the retina. Further evidence that this is so is given later in the paper (p. 81).

The first measurements of the directional sensitivity of the retina were made by photometric methods. The rays from one part of a photometric matching field entered the eye as a narrow pencil through a fixed point of the pupil. The point of entry of the pencil of rays from the other part could be varied. The intensity of this pencil could also be varied so as to bring the two parts to equality of brightness. Thus it was possible to determine the relative physical intensities of rays entering through different points of the pupil and producing the same subjective brightness. The relative luminous efficiency $\eta$ of a ray entering through a particular point of the pupil was defined to be inversely proportional to the physical intensity required to produce a given subjective brightness. It was found (a) that the relative luminous efficiency is maximal for a certain point of entry $P_M$ which is generally situated near the centre of the pupil, (b) that if $\eta$ is put equal to unity for a ray entering at $P_M$ then its value for a ray entering at a point $P$ displaced $r$ mm. from $P_M$ is given approximately by the expression $\eta = 10^{-pr^2}$, where $p$ is a constant equal to about 0.05, (c) that the value of $p$ shows a small systematic variation with wave-length, being greatest in the blue, less in the red and least in the yellow. It was also found that the colour impression produced by monochromatic light of given wave-length varies as the point of entry of the ray is traversed across the pupil.

The results summarized above all refer to foveal vision of a photometric or colorimetric matching field. A different approach to the problem of retinal sensitivity is provided by the measurement of absolute thresholds and difference thresholds. In recent work a type of threshold measurement has been developed on the following lines. The eye views a given distribution of brightness (the conditioning stimulation) and at a given instant, an additional stimulus (the test stimulus) is applied over a given area of the field for a given time. The subject signifies whether or not the application of the test stimulus calls forth any visual impression. No analysis of the visual impression by the subject is required. He has not to decide, for example, whether he perceives a change of brightness or of colour. By successive trials using different intensities of the test stimulus, it is possible to determine the intensity at which the subject has a 50% chance of perceiving the test stimulus. The intensity so obtained is termed the liminal brightness increment (l.b.i.). Usually the test stimulus is a small patch of light exposed for a brief interval of time. With the same conditioning stimulation, the variation of the l.b.i. with a property of the test
stimulus, such as its angular size, its exposure time or, for a monochromatic test stimulus, its wave-length, can be studied. In addition the effect of changes in the conditioning stimulation may be determined. For the purposes of this paper retinal sensitivity will be defined as the reciprocal of the l.b.i.

Measurements of the l.b.i. are much less precise than photometric measurements of brightness. On the other hand, the l.b.i. can be determined for any retinal area, foveal or extrafoveal, and the eye need not be in a steady state. The test stimulus will not in general disturb appreciably the state of adaptation of the retina. This is a valuable feature of the method, enabling us to determine, for example, the sensitivity of the retina to light of one wave-length when it is adapted to light of another wave-length.

In the present investigation the directional sensitivity of the retina has been studied by determining the variation of the l.b.i. as the position in the pupil of the point of entry of the rays constituting the test stimulus is varied. Both foveal and parafoveal vision of the test stimulus were employed. The conditioning stimulation consisted of a uniformly bright circular patch of light at the centre of which the test stimulus was applied. The case in which both test stimulus and conditioning stimulation are of white light has already been examined by Crawford (1937). In the present measurements, small bands of the spectrum were used for both test stimulus and conditioning stimulation. Crawford's results and those of the present paper show that the directional sensitivity of the parafoveal retina is very different for conditioning stimulations of high and low brightnesses respectively. This difference is here attributed to a transition from rod to cone vision as the brightness of the conditioning stimulation is raised. For many of the observations we are able to say whether the test stimulus was perceived by rod or by cone vision by considering the way in which the l.b.i. varies with the wave-length of the test stimulus and the intensity and wave-length of the conditioning stimulation.

The directional sensitivity of the foveal retina shows small but definite variations with the brightness of the conditioning stimulation which appear only for certain combinations of the wave-lengths of test stimulus and conditioning stimulation. These variations are attributed to transitions from vision by one type of cone to vision by another type. It proves possible to distinguish between perception of the test stimulus by different types of cone in foveal vision in much the same way as we distinguish between perception by rods and by cones in parafoveal vision. In the process, we obtain information about the spectral sensitivities of the different types of cone.
2. The subject's conditions of observation

The subject sat in a curtained enclosure and maintained his head in a fixed position by biting on a sealing-wax bit which was rigidly attached to the apparatus. He observed with one eye only, the other eye being covered with an eye shade. His field of view for parafoveal and foveal observation of the test stimulus is shown diagrammatically in figs. 1a and 1b respectively. For parafoveal observation, he directed his gaze at one of the two feeble points of light $F_1$ and $F_2$ (fixation points), the one not in use being removed from the field. For foveal observation, he looked towards the centre of the square of 3° side defined by the four feeble points of light $N_1, N_2, N_3, N_4$ (orientation points). The test stimulus $S$ appeared to him as a square patch of light of 1·04° side, exposed for 0·063 sec. at regular intervals once in every 3·6 sec. For foveal observation, the test stimulus appeared at the centre of the square $N_1N_2N_3N_4$ and for parafoveal observation at a point separated by 5° from the appropriate fixation point and in the position $S$ shown in the figure. An audible signal, repeated just after each exposure, marked time for the subject. The subject held in his hand two keys, one of which he operated when he perceived the test stimulus and the other when he failed to do so.

The conditioning stimulation appeared to the subject as a uniformly bright and approximately circular patch of light of diameter 10° (the central field $C$), outside which the brightness of the field was zero. In an important special case the brightness of this central field was also zero. The test stimulus always appeared in the centre of the central field.

Prior to the commencement of a series of measurements the subject remained in the dark for a period up to 1 hr. depending on the nature of the measurements. The pupil of his observing eye was dilated when necessary by administering a few drops of a 5 % solution of euphthalmine hydrochloride about 1 hr. before the measurements.

3. Apparatus and method

The main principle of the apparatus is made clear by fig. 2. A parallel beam of light provided by spectrometer II is partially transmitted by the cube $C$ and is brought to a focus $O_2$ in the plane of the subject's pupil at $O$ by the lens $L_3$. This beam is seen by the subject as a uniformly bright patch of light which forms the central field of the conditioning stimulation. A parallel beam from spectrometer I is delimited by a square aperture in the diaphragm $T_3$, is partially reflected at the diagonal surface in the cube $C'$
and is finally brought to a focus $\omega_1$ in the plane of the subject's pupil by the lens $L_3$. The diaphragm $T_3$ is so placed that the subject sees a virtual image of the square aperture at infinity. This image forms the test stimulus. It is important to note that in the area of the field of view occupied by the test stimulus, the eye receives radiation from both the test stimulus and the conditioning stimulation; thus in this sense, the test stimulus is added to or superposed on the conditioning stimulation. The fixation and orientation points are introduced from the side by reflexion in a thin plain glass plate $M$ inserted in the parallel beam from spectrometer $\Pi$. The rays forming a particular fixation or orientation point are reflected by $M$ to form a real image in the plane $K$ which is the focal plane of the lens $L_3$. This real image when seen through the lens $L_3$ appears to the subject as a virtual image at infinity.

By slight rotations of the cube $C$ the test stimulus beam can be sent into the eye through different points of the pupil, while the point of entry of the beam forming the central field remains practically unchanged. After such a rotation of cube $C$, the diaphragm $T_3$ must be readjusted by a displacement in its own plane to restore the test stimulus to its original position in the subject's field of view.

A diagram of the complete apparatus is shown in fig. 3. As the apparatus differs little from that described in a previous paper (Stiles 1937), it will suffice to indicate its main features and such changes and additions as have been made.

Images of the ribbon filament source $S_1$ are formed on the entrance slits of the two spectrometers $I$ and $\Pi$. The rays from the exit slit of spectrometer $I$ pass through the continuous wedge $W_1$ and the step-wedge $W_2$ and are rendered parallel by the lens $L_2$. The rays from the exit slit of spectrometer $\Pi$ pass through the continuous wedge $W_3$ and are rendered parallel by lens $L_4$. The two parallel beams from the spectrometers are then focused to give images $\omega_1$ and $\omega_2$ of the respective exit slits at the subject's eye, as already explained. The auxiliary optical system $L_7-G-E$ enables the relative positions of the slit images to be determined without disturbing the subject.

At $R_1$ a shutter is interposed in the beam of spectrometer $I$. The shutter consists of two rotating disks geared together so that one rotates three times for each rotation of the other. There is an indentation in the periphery of each disk and light is passed by the shutter only when the two indentations come into coincidence opposite the entrance slit of the spectrometer. The width of the indentation in the faster disk, the radius of this disk and its speed of rotation determine the exposure time of the test
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FIG. 1. Subject's field of view (a) for parafoveal, (b) for foveal observation.

FIG. 2. Diagram showing the principle of the measurements.

FIG. 3. Diagram of the apparatus (not to scale).

FIG. 4. Derivation of $A$.

FIG. 5. Directional sensitivity of the dark-adapted parafovea (fixation point $F_1$).

FIG. 6. Directional sensitivity of the dark-adapted fovea.
stimulus. The use of two disks in this way, rather than a single disk, gives a shutter of higher efficiency. The slower disk carries contacts operating a buzzer once in every 3-6 sec.

The thread controlling the position of the step wedge \( W_2 \) is connected to a carriage moving on rails across a wide strip of recording paper which is given a slow motion in the direction of its length. Two pens, marking in different colours and operated by the keys in the subject's hands, are fixed to the carriage. Between successive exposures of the test stimulus the carriage is moved to bring different steps of the wedge \( W_2 \) into the beam so that on the paper a record is obtained of the subject's responses to different intensities of the test stimulus.

Stray light filters and neutral filters can be inserted in the beam of spectrometer I, of spectrometer II or in the common beam at \( F_1, F_{II}, F_c \) respectively.

The fixation or orientation points are obtained in the following manner. An opal lamp \( S_2 \) placed at the focus of lens \( L_8 \), the image being at the focus of lens \( L_{10} \), so that finally an image of the lamp is formed on the eye by the lens \( L_9 \). Between lenses \( L_8 \) and \( L_9 \) a metal diaphragm \( T_4 \) is inserted containing one or four small holes (fixation or orientation points respectively). The images of these holes formed by lens \( L_{10} \) are arranged to lie in the focal plane of lens \( L_3 \) (allowing for reflection in \( M \)) so that the subject sees the fixation or orientation points at infinity. A resistance enables the subject to adjust the intensity of the lamp \( S_2 \) and colour filters can be inserted in the beam if required.

The positioning of the eye with respect to the slit images \( \omega_1 \) and \( \omega_2 \) and the measurement of the separation of \( \omega_1 \) and \( \omega_2 \) were carried out by methods similar to those previously described. When filters were inserted at \( F_c \), a slight displacement of the images \( \omega_1 \) and \( \omega_2 \) usually occurred. The images were restored to their correct positions by a suitable shift of the lens \( L_3 \) in its own plane.

The method of calculating the intensities of the areas of the subject's field of view illuminated by the two spectrometers was the same as in the previous investigation. The calculations yield the values of the following quantities:

\[ U'_\lambda = \text{the flux of radiant energy of wave-length } \lambda, \text{ expressed in ergs/sec., received by the eye from spectrometer I during the exposure of the test stimulus, divided by the angular area of the test stimulus expressed in square degrees.} \]

(For brevity \( U'_\lambda \) will be referred to as the "energy" of the test stimulus.)
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$W_\mu$ = the flux of radiant energy of wave-length $\mu$, expressed in ergs/sec., received by the eye from spectrometer II divided by the area in square degrees of the field illuminated by spectrometer II. ($W_\mu$ will be referred to as the energy of the central field.)

Corresponding to $U'_\lambda$ and $W_\mu$, the conventional photometric brightnesses $B'_U$ and $B_W$ of the test stimulus and central field are derived from the relations:

$$B'_U = 2.02 \times 10^3 U'_\lambda V_\lambda,$$
$$B_W = 2.02 \times 10^3 W_\mu V_\mu,$$

where $V_\lambda$ and $V_\mu$ are the values of the standard relative luminosity factor for wave-lengths $\lambda$ and $\mu$ respectively. $B'_U$ is defined as the brightness in candles per square foot which, if viewed through an artificial pupil of area 10 sq. mm. by an eye possessing the standard curve of relative luminosity, would match in brightness the test stimulus as seen by a similar eye in the actual apparatus. $B_W$ is similarly defined.*

The spectral purity of the light in test stimulus or central field is specified by the wave-length difference $\Delta \lambda$ or $\Delta \mu$ between the extreme limits of the spectrum band passed by the spectrometer. In general, $\Delta \lambda$ and $\Delta \mu$ had values of the order of 15 and 30 m$\mu$ respectively. Parasitic light of wave-length lying outside the desired band was reduced to an unimportant amount by the use of coloured stray-light filters.

For the exit slit of spectrometer I a fixed slit of height 0.50 mm. and width 0.48 mm. was used for all the measurements. The image $\omega_1$ of this slit had the same dimensions. For the entrance slit, fixed slits of various widths were used. The slit height of spectrometer II was either approx. 0.50 or 2.20 mm. The continuously variable symmetrical slits were adjusted as required.

The calculations of $U'_\lambda$ and $W_\mu$ were made assuming the slit widths so small that slit-width corrections could be neglected.

4. Derivation of the liminal brightness increment from the record of the subject’s responses

The logarithm of the energy of the test stimulus during a measurement of the l.b.i. may be expressed in the form

$$\log_{10} U'_\lambda = \log_{10} (U'_\lambda)_0 - A_n,$$

* $B'_0$ and $B_w$ can be obtained in terms of photons by replacing the factor $2.02 \times 10^3$ by $2.18 \times 10^5$. 

(* This footnote should be placed before the equation it refers to, not after.)*
where \((U\lambda)_0\) is the energy when the step wedge \(W_2\) was removed from the beam the other conditions remaining unchanged, and \(\Lambda_n\) is the optical density for wave-length \(\lambda\) of the \(n\)th step of wedge \(W_2\). If the subject recorded "seen" \(M\) times, and "not seen" \(N-M\) times when a particular step of \(W_2\) was in the beam, then \(f = M/N\) may be regarded as an approximation to the probability of seeing the test stimulus for that particular energy. Determinations of \(f\) for a series of consecutive values of \(n\) gave a graph of \(f\) against \(\Lambda_n\) from which the l.b.i. could be derived. Examples of such graphs are shown in fig. 4. In each case five exposures were made at each step, i.e. \(N = 5\). The density difference between consecutive steps equalled approximately 0.07 but varied slightly with wave-length. The \(S\)-shaped curves drawn in fig. 4 are all of the form:

\[
\begin{align*}
f &= \frac{1}{2}[1 - P\{h(\Lambda_n - \Delta)\}] \quad \text{for } \Lambda_n > \Delta \\
 &= \frac{1}{2}[1 + P\{h(\Lambda_n - \Delta)\}] \quad \text{for } \Lambda_n < \Delta,
\end{align*}
\]

in which \(\Lambda_n\) is allowed to vary continuously, \(\Delta\) and \(h\) are constants, and \(P\{x\}\) is the probability integral \(\sqrt{\pi} \int_0^x e^{-z^2} \, dz\). A relation between \(f\) and \(\Lambda_n\) of this form is to be expected if the following conditions hold:

(i) when the test stimulus is exposed there is a critical intensity which must be exceeded if the subject is to record "seen",

(ii) the critical intensity varies from exposure to exposure in a random manner about an average value corresponding to a density in the beam equal to \(\Delta\),

(iii) if \(\Delta', \Delta'', \Delta''', \text{etc.}\) are the densities corresponding to the critical intensities at the instants of different exposures, then \(\Delta', \Delta'', \Delta''', \text{etc.}\), form a Gaussian distribution about a mean value \(\Delta\) with a modulus of precision \(h\).

In most cases an \(S\)-shaped curve of the above form could be fitted to the plot of \(f\) against \(\Lambda_n\) with the measure of agreement illustrated in fig. 4.

In practice, tracings of the theoretical \(S\)-shaped curve corresponding to different values of \(h\) were prepared. The traced curves could be placed in turn over the experimental graph of \(f\) against \(\Lambda_n\) and the pair of values of \(h\) and \(\Delta\) giving the best fit could be determined "by inspection".

The energy \(U\lambda\) of the test stimulus corresponding to the density value \(\Delta\) is given by the relation

\[\log_{10} U\lambda = \log_{10} (U\lambda)_0 - \Delta.\]

\(U\lambda\) is the energy of the test stimulus at which the subject’s response is as likely to be "seen" as "not seen". \(U\lambda\) is accepted as the value of the l.b.i. yielded by the measurement. Corresponding to each determination of \(U\lambda\)
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we obtain in h an estimate of the sharpness of the liminal value, or of the extent to which the critical intensity referred to in (i) above varies from exposure to exposure.

In the first measurements a determination of the l.b.i. was based on sixty exposures, made up of five exposures each of nine consecutive steps of wedge \( W_2 \), which were known from a preliminary rough setting by the subject to embrace the liminal value, together with fifteen blanks (test stimuli of zero intensity). The sixty exposures were presented in random order. It was soon found that a "seen" response to a blank was obtained only very rarely. For the bulk of the measurements the stimuli were presented in order of decreasing or increasing intensity, the step wedge being moved one step after each exposure. Each succession of exposures covered the range from "certainly seen" to "certainly not seen" or vice versa. Three successions of exposures with increasing intensity and two with decreasing intensity completed the measurement. No blanks were included. Tests showed that this method gave about the same values of the l.b.i. as the first method but the precision was a little better; it imposed less strain on the subject and called for a less precise preliminary setting. It was adhered to for all the subsequent measurements.

5. Specification of the direction of incidence of a ray on the retina

The direction of incidence on the retina is the effective variable determining the change in retinal response when a ray enters the eye through different points of the pupil. As in previous work, this direction will be specified indirectly by giving the position of the point of entry of the ray in the pupil or rather in the apparent pupil, i.e. the pupil seen from outside the eye. The ray entering through the centre of the apparent pupil and terminating on a given retinal point may be regarded as defining the normal to the retina at that point. Any other ray entering the apparent pupil at a point \( d \) mm. from the centre and terminating on the same retinal point will strike the retina at an angle of incidence (i.e. at an angle with the normal ray) equal to \( 2.4d \) deg. This result is only a rough approximation applicable for an average normal eye and for retinal points at or near the fovea. Since for the fully dilated pupil \( d \) may have a value up to about 4 mm., we are dealing with the effects of changing the angle of incidence from 0° to about 10°.

There are practical advantages in keeping the point of entry on the horizontal diameter of the apparent pupil and this has been done in all the
present measurements. Thus we require only one variable, namely \( d \), the
distance in mm. from the point of entry to the centre of the apparent pupil,
\( d \) is taken as positive when the point of entry is on the temporal and
negative when it is on the nasal side of the centre. It is easy to show that
when the relative luminous efficiency \( \eta \) can be represented by the expression
\( 10^{-pr^2} \), where \( r \) is the distance in mm. of the actual point of entry from the
point of entry \( P_M \) giving maximal luminous efficiency, then the variation
of \( \eta \) across the horizontal diameter is represented by the analogous ex-
pression \( 10^{-p(d-d_m)^2} \), where \( p \) has the same value as before and \( d_m \) defines
the position of the point of entry which gives a greater luminous efficiency
than any other point on the horizontal diameter.

The pupil is not a fixed structure in the eye. Its diameter and, possibly,
the position of its centre change with the lighting conditions. It appears
from the present measurements that, when dilated with a mydriatic, the
pupil does not always assume the same diameter. The centre of the dilated
pupil has been found to shift slightly ( \( \frac{1}{10} \) to \( \frac{3}{10} \) mm.) during the course of a
series of measurements. These vagaries are unfortunate for the present
purpose.*

6. RESULTS. CENTRAL FIELD OF ZERO BRIGHTNESS

All the measurements reported refer to the writer’s left eye. This is a
slightly hypermetropic eye (\(+0.5\) Sph. \(-0.25\) Cyl. 130°) and a normal
trichromat belonging to Abney and Watson’s Class I (rod-free fovea). The
examination of other eyes was deferred until the results of the present work
should have indicated the points meriting special study.

We consider first the case in which the subject’s field of view was com-
pletely dark save for the fixation or orientation points and the flashes of the
test stimulus. Prior to every series of measurements the subject remained
for about 1 hr. in the dark. Thus the observations were made with the
dark-adapted eye. Fig. 5 shows, for five wave-lengths of the test stimulus,
the variation of the logarithm of the l.b.i. for 5° parafoveal vision (fixation
point \( F_1 \)) as the point of entry of the rays was moved across the horizontal
diameter of the apparent pupil. Each plotted point is the mean of two or
more values obtained in independent runs. In each run half the points
were obtained in a traverse from nasal to temporal, the other half in a
traverse in the reverse sense. At present we are concerned only with the

* A method of specifying point of entry independently of the pupil has been
suggested to the writer by Professor Hartridge. The proposal is to use as a fixed point
of reference in the eye the reflected image in the cornea of a distant light on which the
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variation of \( \log_{10} U_{\lambda} \) and an arbitrary constant has been added to the absolute values for each curve to give a convenient spacing of the different curves in the figure. In the figure the scale of \( \log_{10} U_{\lambda} \) has been taken to be increasing in the downwards direction, so that the curves represent the variation of \( -\log_{10} U_{\lambda} = \log_{10} 1/U_{\lambda} \) with respect to a similar scale increasing in the upwards direction. The curves show that the sensitivity of the dark-adapted parafoveal retina is practically non-directional for test stimuli in the blue-green but exhibits a slight directional effect in the yellow, which becomes well defined in passing through orange to red. In the violet there appears to be a slight effect in the reverse sense.

Similar measurements for foveal vision of the test stimulus are given in fig. 6. The familiar difficulties in measuring the foveal threshold (save in the red end of the spectrum), due to the greater sensitivity of the parafovea, are accentuated when the rays enter near the edge of the pupil. This is so because the parafoveal sensitivity is maintained while the foveal sensitivity falls off as the point of entry moves from centre to periphery of the pupil.

Fortunately with practice the subject can tell from the appearance of the test stimulus whether his fixation has wandered so that he is using parafoveal instead of foveal vision. When this occurred, the subject operated neither key and the exposure was repeated. It sometimes happened when the test stimulus was correctly fixated, that the light scattered or irregularly reflected in the eye could be seen parafoveally although the normal image of the test stimulus produced no response. This was not accepted as vision of the test stimulus.

The curves of fig. 6 show that the sensitivity of the dark-adapted foveal retina exhibits a pronounced directional effect whatever the wave-length of the test stimulus.

It is appropriate to compare the variation of \( \log_{10} (1/U_{\lambda}) \) with point of entry and the corresponding variation of \( \log_{10} \eta \), where \( \eta \) is the relative luminous efficiency obtained in brightness matching measurements. The variation of \( \log_{10} (1/U_{\lambda}) \) can in fact be represented to a first approximation by the empirical formula:

\[
\log_{10} (1/U_{\lambda}) = \log_{10} (1/U_{\lambda})_m - p_{\lambda}(d-d_m)^2, \tag{1}
\]

where \( \log_{10} (1/U_{\lambda})_m \) is the maximum value of \( \log_{10} (1/U_{\lambda}) \) which is attained at \( d = d_m \), and \( p_{\lambda} \) is a constant. This formula is of the same form as that previously found for \( \log_{10} \eta \) and there can be little doubt that the same cause is operative in the two types of experiment. The continuous curves drawn in figs. 5 and 6 have been computed from the above formula with suitable
choice of the constants $p_\lambda$ and $d_m$. For the foveal measurements, the data show a tendency (very marked for $\lambda = 430$ m$\mu$) to deviate from the fitted curve for $(d - d_m)$ greater than 3 mm. A similar deviation was observed in the curves of $\log_{10} \eta$ against $d$. The values of $p_\lambda$ for foveal vision come out to be about 15% lower than those derived from the $\log_{10} \eta$ curves obtained for the same eye in the brightness matching experiments with monochromatic light (Stiles 1937). The position of the maximum $d_m$ is also displaced from about 0.6 mm. temporal to about 0.9 mm. temporal.

To see whether these differences were due to a difference in the luminous efficiencies operative for the threshold measurements and for the brightness matching measurements, or to an actual change in the eye, brightness matching traverses were made for $\lambda = 500$ m$\mu$ and for $\lambda = 700$ m$\mu$ (foveal vision). The results gave values of $p_\lambda$ and $d_m$ in substantial agreement with those found from the corresponding threshold curves. It must be concluded that for this eye the direction of incidence on the retina of the ray giving maximal luminous effect and the magnitude of the directional effect specified by $p_\lambda$ have changed. Changes of the same kind are in evidence if the measurements of $\eta$ made with monochromatic light (Stiles 1937) are compared with the original measurements made with white light (Stiles and Crawford 1933). It appears that in the course of about six years the point of entry in the horizontal diameter giving the greatest value of $\eta$ has shifted for this eye from about 0.2 mm. nasal to about 1.0 mm. temporal. Whatever the actual mechanism giving rise to the directional properties of the retina, we are probably justified in regarding the direction of incidence which gives the greatest value of $\eta$ as defining in some manner the direction in which the end organs of the retina are pointing. It is possible therefore that for the eye in question the end organs at the fovea are being gradually sheared over. During about the same period of time the refraction of the eye has changed from emmetropic to $+0.5$ Sph. $-0.25$ Cyl. 130° but no other symptom which might possibly be correlated with the changes in $d_m$ has been noted.

The values of $d_m$ for several eyes studied by Crawford and the writer are given in Table I. In some cases the point of entry was varied on the vertical diameter of the pupil and $d_m$ then defines the position on the vertical diameter giving the greatest value of $\eta$. The values of $d_m$ for extrafoveal points were obtained from measurements of the l.b.i.

Unfortunately the pupil centre is not a perfectly stable reference point and the value of $d_m$ is subject to some ambiguity on this account. However, the figures in the table show that $d_m$ varies appreciably for different eyes, and for different retinal points of the same eye. The systematic
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Table I. Position of the point of entry on the horizontal or vertical diameter of the pupil of the ray giving the greatest visual effect

<table>
<thead>
<tr>
<th>Subject</th>
<th>Date of measurement and reference</th>
<th>Method of measurement</th>
<th>Retinal patch</th>
<th>Diam. of pupil traversed</th>
<th>( d_m ) in mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>L.E. = left eye, R.E. = right eye</td>
<td>1932 (1)</td>
<td>Brightness matching</td>
<td>Fovea</td>
<td>Hor.</td>
<td>-0.2 (nasal)</td>
</tr>
<tr>
<td></td>
<td>1932 (1)</td>
<td></td>
<td></td>
<td>Vert.</td>
<td>-0.5 (upper)</td>
</tr>
<tr>
<td></td>
<td>1932* (1)</td>
<td></td>
<td></td>
<td>Hor.</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>1932 (1)</td>
<td></td>
<td></td>
<td>Vert.</td>
<td>-0.2 (upper)</td>
</tr>
<tr>
<td></td>
<td>1936 (2)</td>
<td></td>
<td></td>
<td>Hor.</td>
<td>+0.6 (temp.)</td>
</tr>
<tr>
<td></td>
<td>1936 (2)</td>
<td></td>
<td></td>
<td>Vert.</td>
<td>-0.5 (upper)</td>
</tr>
<tr>
<td></td>
<td>1937–8 (4)</td>
<td></td>
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<td>Hor.</td>
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<td>Fovea</td>
<td>Hor.</td>
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<td>Vert.</td>
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<td>-1.5 (nasal)</td>
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<td>-1.8 (nasal)</td>
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* Six weeks later.

References: (1) Stiles and Crawford (1933); (2) Stiles (1937); (3) Crawford (1937); (4) Stiles (present work).

determination of \( d_m \) in the vertical and horizontal diameters for a large number of eyes would be of considerable interest.

Further measurements of the effect of wave-length on the directional sensitivity were made by the two-point method, in which \( \log_{10} U_\lambda \) is determined for two points of entry, \( P_o \), at or near the point giving maximal sensitivity (central entry) and \( P_p \), near the periphery of the pupil (peripheral entry). Measurements were made for a series of wave-lengths spanning the spectrum in one run. From the two values of \( \log_{10} U_\lambda \) obtained for
each wave-length and from the co-ordinates \( d_o \) and \( d_p \) of the points \( P_o \) and \( P_p \), the value of \( p_\lambda \) was computed using formula (1). It was necessary to assume the value of \( d_m \) obtained earlier from the curves of figs. 5 and 6.

Figs. 7 and 8 give the mean values of \( p_\lambda \) obtained from five two-point determinations for parafoveal vision and from three such runs for foveal vision. For parafoveal vision, \( p_\lambda \) is not very different from zero for \( \lambda \) less than 600 m\(\mu\). As \( \lambda \) increases from 600 to 700 m\(\mu\), \( p_\lambda \) increases to approximately 0.045 and finally it appears to drop again slightly. For foveal vision \( p_\lambda \) lies in the range 0.045 to 0.065 and shows a variation with wave-length similar to that found previously in the brightness-matching experiments. The values of \( p_\lambda \) obtained from new measurements by the brightness-matching method (two point determinations) are shown as the circles in fig. 9 which also gives the values obtained in the earlier investigation. Apart from the shift in absolute value already noted, the new determinations of \( p_\lambda \) by the brightness-matching method show the same variation with wave-length as the old and this variation is closely followed by the values of \( p_\lambda \) derived from the l.b.i. determinations.

Determination of \( p_\lambda \) at a second parafoveal point, again at 5° from the fovea, but in a different meridian, are plotted in fig. 10. For these measurements the fixation point \( P'_2 \) was used. Save for the point at \( \lambda = 450 \) m\(\mu\), \( p_\lambda \) shows a similar variation with wave-length to that obtained for the other parafoveal point. For this parafoveal point, \( d_m \) had the value 1.5 mm. (temporal).

We may sum up the above results as follows: the sensitivity of the dark-adapted parafovea is nearly independent of the direction of incidence of the light on the retina except for wave-lengths in the orange and red. The sensitivity of the dark-adapted fovea shows a pronounced variation with direction of incidence for all wave-lengths. The magnitude of the directional effect for the fovea varies to a limited extent with wave-length and the variation resembles that found in the earlier experiments by the brightness-matching method.

In parafoveal observation of a coloured test stimulus, the fact that the test stimulus is coloured can be appreciated only when its intensity exceeds a certain multiple of the threshold value. This multiple, known as the photochromatic ratio, was observed to be greater for peripheral entry than for central entry of the light rays in the pupil. For example, at 700 m\(\mu\) it had on the average the value 1.4 for central, and 2.5 for peripheral entry. At shorter wave-lengths, the values were of course very much larger but showed a difference in the same sense between central and peripheral entry.
The directional sensitivity of the retina

Fig. 7. Variation of $p_\lambda$ with $\lambda$ for the dark-adapted parafovea ($F_1$). $\bigcirc$, Two-point determinations; $\times$, from data of fig. 5.

Fig. 8. Variation of $p_\lambda$ with $\lambda$ for the dark-adapted fovea. $\bigcirc$, Two-point determinations; $\times$, from data of fig. 6.

Fig. 9. Variation of $p_\lambda$ with $\lambda$ by brightness-matching method. $\bigcirc$, New values by two-point method; $\square$, new values from traverses; $\times$, old values, Stiles (1937).

Fig. 10. Variation of $p_\lambda$ with $\lambda$ for the dark-adapted parafovea ($F_2$). $\bigcirc$, Two-point method (single determination); $\square$, from traverses.

Fig. 11. Spectral sensitivities of dark-adapted fovea and parafovea ($F_1$). Central entry.

Fig. 12. Directional sensitivity of the light-adapted parafovea ($F_1$). $\lambda = \mu$; $\log_{10} W_{\mu}$ round about 2.5. $\square$, From traverses of fig. 12.
In foveal observation of the test stimulus, the photochromatic ratio does not depend on the point of entry and, in fact, it has the value 1 for all colours except yellow.

The mean values of $\log_{10} U_\lambda$ for central entry, obtained in the two-point determinations, are plotted against wave-length in fig. 11. The actual values are given and not the values plus an arbitrary constant as in figs. 5 and 6. The curves of fig. 11 are of the type first obtained by Abney and Watson (1916) and they can be interpreted in terms of the duplicity theory of vision in the following manner. Foveal vision of the test stimulus is served solely by the cones since rods are absent from the fovea. Thus the foveal curve represents the variation with wave-length of the logarithm of the l.b.i. of the foveal cone system. The parafovea contains both rods and cones. For any wave-length of the test stimulus the parafoveal rods acting alone would give one value of the l.b.i., $(U_\lambda)_s$, and the parafoveal cones acting alone would give another value $(U_\lambda)_p$. The l.b.i. of the parafoveal cones may be assumed to vary with wave-length in much the same way as the l.b.i. of the foveal cones so that the graph of $\log_{10} (U_\lambda)_p$ against $\lambda$ will have the same form as the foveal curve of fig. 11 although it may be displaced parallel to the axis of $\log_{10} U_\lambda$. In reality the rods and cones are in action together and although we do not know how their respective effects “add up” we may safely assume that the resultant parafoveal l.b.i. will not be greater than either $(U_\lambda)_s$ or $(U_\lambda)_p$. Thus since for $\lambda$ greater than 630 m$\mu$ the parafoveal l.b.i. exceeds the foveal l.b.i., it follows a fortiori that $(U_\lambda)_p$ will exceed the foveal l.b.i. This means that the parafoveal cone system is less sensitive than the foveal cone system. On the other hand for $\lambda$ less than 600 m$\mu$, the parafoveal l.b.i. is much smaller than the foveal l.b.i. and, a fortiori, much smaller than $(U_\lambda)_p$. Thus in this region of the spectrum we can identify the parafoveal l.b.i. with $(U_\lambda)_s$, the l.b.i. of the parafoveal rod system. As $\lambda$ increases beyond 600 m$\mu$ it is probable that the ratio of $(U_\lambda)_p$ to $(U_\lambda)_s$ tends to diminish, until at 700 m$\mu$ the two quantities are not very different. This is suggested by the fact that the photochromatic ratio for parafoveal vision diminishes for $\lambda$ greater than 600 m$\mu$, until at $\lambda = 700$ m$\mu$ it equals approximately 1.4. Thus, the parafoveal cones may participate to an increasing degree in determining the parafoveal l.b.i. as we pass from 600 m$\mu$ to the extreme red end of the spectrum.

If we accept the above interpretation, then in fig. 8 the values of $p_\lambda$ measure the directional sensitivity of the foveal cones. In fig. 7 the values of $p_\lambda$ for $\lambda$ less than 600 m$\mu$ measure the directional sensitivity of the parafoveal rods. The increase in $p_\lambda$ at longer wave-lengths may be due (a) to an increase in the directional sensitivity of the parafoveal rods with increase
The directional sensitivity of the retina

in wave-length, (b) to the participation of the parafoveal cones which, like
the foveal cones, may show a large directional sensitivity at all wave-
lenghts, (c) to a combination of these two causes.

7. CENTRAL FIELD ILLUMINATED: PARAFOVEA

For all the observations described in this section, the light rays forming
the central field entered the subject’s eye through the centre of the pupil.
The test stimulus was observed parafoveally using fixation point $F_1$. With
a central field of high brightness and of the same wave-length as the test
stimulus, the variation of $\log_{10} U_{\lambda}$ with point of entry of the test stimulus
was determined for wave-lengths 500, 580 and 690 m$\mu$ (fig. 12). The values
of $p_{\lambda}$ obtained from two-point determinations under similar conditions are
plotted against $\lambda$ in fig. 13. These results show that when the parafoveal
retina is adapted to a high brightness of given wave-length, it exhibits a
well-developed directional sensitivity to a test stimulus of the same wave-
length whatever that wave-length may be.

The differences in the directional sensitivities of the light- and dark-
adapted parafoveal retina, which are evident from a comparison of figs. 5
and 12 or 7 and 13, prove conclusively that we are in fact dealing with the
directional properties of the retina and not with differences in light losses in
the refractive system of the eye. Effects of the latter kind would be un-
affected by the presence or absence of the central field.

By determining $\log_{10} U_{\lambda}$ for central and peripheral entry of the test stimu-
lus at a series of brightnesses of the central field from zero upwards the
change in directional sensitivity with brightness level could be followed.
The subject remained in the dark for 1 hr. before each run, his pupil
having been previously dilated with euphthalmine. The mean results of
two runs at each of the wave-lengths 500, 580 and 690 m$\mu$ are plotted in
figs. 14, 15 and 16. Each figure gives three curves:

I. $\log_{10} U_{\lambda}$ against $\log_{10} W_{\mu}$ for central entry of the test stimulus.

II. $\log_{10} U_{\lambda}$ against $\log_{10} W_{\mu}$ for peripheral entry of the test stimulus.

III. $p_{\lambda}$ against $\log_{10} W_{\mu}$ derived from the previous curves by applying
formula (1).

Consider first fig. 15 for which $\lambda = \mu = 580$ m$\mu$. The curve of $p_{\lambda}$ against
$\log_{10} W_{\mu}$ falls into a low brightness region in which $p_{\lambda}$ is approximately con-
tant and small, a transitional region in which $p_{\lambda}$ increases with $\log_{10} W_{\mu}$, and
a high brightness region in which $p_{\lambda}$ is again approximately constant but has
a high value. Turning to the curves of $\log_{10} U_{\lambda}$ against $\log_{10} W_{\mu}$, we note that
to begin with the gradient of curve I increases with \( \log_{10} W \) and approaches a constant value. Then at about the beginning of the transitional region the gradient decreases with increase in \( \log_{10} W \). Subsequently it increases again and finally approaches a constant value. Curve II behaves similarly except that the decrease in the gradient of the curve occurs at about the end of the transitional region. Graphs of the logarithm of the parafoveal l.b.i. against the logarithm of the conditioning brightness exhibiting a “change of law” of this kind were first observed using white light for both test stimulus and conditioning stimulation and their interpretation in terms of the duplicity theory has already been given (Stiles and Crawford 1932, 1934). It is assumed that if we could determine the l.b.i. \((U_{\lambda})_s\) of the rod system acting alone we should obtain a curve of \( \log_{10} (U_{\lambda})_s \) against \( \log_{10} W \) similar to curve A of fig. 17. The cone system acting alone would give, on the other hand, a curve of \( \log_{10} (U_{\lambda})_p \) against \( \log_{10} W \) similar to curve B. In the practical case when both systems are in action, the measured \( \log_{10} U_{\lambda} \) would coincide with \( \log_{10} (U_{\lambda})_s \) at low brightnesses where \( \log_{10} (U_{\lambda})_s \) is considerably smaller than \( \log_{10} (U_{\lambda})_p \), and with \( \log_{10} (U_{\lambda})_p \) at high brightnesses where the reverse is true. In the neighbourhood of the point of intersection of curves A and B, where \( \log_{10} (U_{\lambda})_s \) and \( \log_{10} (U_{\lambda})_p \) have comparable values the observed \( \log_{10} U_{\lambda} \) would be smaller than either so that the experimental curve would follow some such course as that indicated by the dotted line C. Curve C is made up of three sections: a rod section at low brightnesses where C is coincident with A, a cone section at high brightnesses where C is coincident with B and a mixed section at intermediate brightnesses where C lies below both the curves A and B.

Accepting the view that the change of law in curves I and II of fig. 15 is produced in the way just described, we obtain a simple explanation of curve III. Suppose in fig. 17, curves A and B refer to central entry of the test stimulus. Assume now that the rods show no directional sensitivity at any brightness of the central field. Curve A will then apply equally for peripheral and central entry.* Suppose, on the other hand, that the cones show a pronounced and constant directional sensitivity at all brightness levels. Then the curve of \( \log_{10} (U_{\lambda})_p \) against \( \log_{10} W \) for peripheral entry of the test stimulus (curve B’) will have the same shape as curve B but will be

* Since \( p_{\lambda} \) has a small positive value in the low brightness region of curve III (fig. 15), the rods probably show a slight directional effect when stimulated with \( \lambda = 580 \text{ m\AA} \). For simplicity this effect has been ignored in constructing the curves of fig. 17 which are primarily intended to illustrate the principle of the suggested explanation.
The directional sensitivity of the retina

FIG. 14

Fig. 17. Explanation of the results for parafoveal vision, in terms of the duplicity theory.

FIG. 15

Figs. 14–16. For key see p. 81 of text.

FIG. 16

Fig. 18. Alternative explanations of the results for red light. In (b), A and A’ refer to the rods and to central and peripheral entry respectively.
displaced parallel to the axis of $\log_{10}(U)$ to higher values. The resultant curve of $\log_{10}U_\lambda$ against $\log_{10}W_\mu$ when both rod and cone systems are in operation will be represented for peripheral entry by curve $C'$. By taking the difference of curves $C'$ and $C$ and applying formula (1) we obtain the variation of $p_\lambda$ with $\log_{10}W_\mu$ as curve $D$.

The main features of the experimental curves of fig. 15 are all reproduced in the corresponding curves $C$, $C'$ and $D$ of fig. 17. For this case the duality theory, together with the assumption of constant directional sensitivities for the rod and cone systems, provides a possible explanation of the change in directional sensitivity with brightness level.

The experimental curves for $\lambda = \mu = 500$ m$\mu$ (fig. 14) are generally similar to those for $\lambda = \mu = 580$ m$\mu$ and may be similarly explained. There are differences, however. The transitional region in curve III extends over a wider range, and the change of law in the curves of $\log_{10}U_\lambda$ against $\log_{10}W_\mu$ is observable only for curve I. These differences may be due to the rod and cone curves $A$ and $B$ (fig. 17) being so displaced that they intersect at a smaller angle.

For $\lambda = \mu = 690$ m$\mu$ (fig. 16), we may apply the above explanation in the way shown schematically in fig. 18a. There is an alternative possibility however; the rods when stimulated with red light may exhibit a well-developed directional sensitivity, although a smaller one than the cones. The scheme of fig. 18b would then apply. We are faced here with the uncertainty to which reference was made at the end of the previous section.

The more general case when test stimulus and central field have different wave-lengths will now be examined. Figs. 19 and 20 give respectively the results of two-point determinations for the combinations $\lambda = 580$, $\mu = 500$ and $\lambda = 450$, $\mu = 520$. With these combinations the transition from rod to cone vision in curves I and II and the corresponding change in the directional sensitivity measured by $p_\lambda$ are very clearly shown. The results are in good accord with the explanation illustrated by the curves of fig. 17.

With the combination $\lambda = 500$, $\mu = 690$, the results are of a different character (fig. 21). Despite the large scatter in the experimental values we may admit that on the whole there is no systematic variation of $p_\lambda$ with brightness level. The curve relating $\log_{10}U_\lambda$ and $\log_{10}W_\mu$ is nearly the same for central and peripheral entry and a “change of law” of the kind previously obtained is not in evidence. These facts suggest that at all values of $\log_{10}W_\mu$, the test stimulus is seen by rod vision. In our view this result is obtained because the rod curve (curve $A$, fig. 17) lies below and to the right of the two cone curves ($B$ and $B'$, fig. 17) and does not intersect them. The results for the combination $\lambda = 500$, $\mu = 660$ (fig. 22) allow of a similar
The directional sensitivity of the retina

Figs. 19-23. Key as for figs. 14-16.
interpretation, except that at the highest brightness level $p_\lambda$ rises sharply. This rise is believed to be genuine but its explanation depends on a new factor to be dealt with later.

The interpretation of the results may now be carried a stage further. For each combination of $\lambda$ and $\mu$, we have envisaged a rod curve $A$ and a cone curve $B$, but nothing has been said of the connection between the rod curves or the cone curves for different combinations. In the brightness range where curves I and II of fig. 22 are indistinguishable, the common curve according to our interpretation is purely a rod curve. A tracing of this curve can be fitted approximately over the rod sections of all the experimental curves of $\log_{10}U_\lambda$ against $\log_{10}W_\mu$* which possess an identifiable rod section. Thus to a first approximation the rod curve has the same shape for all combinations $\lambda$ and $\mu$ for which it can be observed and is merely displaced (without rotation) to different positions with respect to the axes. Moreover, for two combinations with the same $\mu$ but different $\lambda$'s the rod curves are found to have approximately the same positions with respect to the axis of $\log_{10}W_\mu$ but are relatively displaced in a direction parallel to the axis of $\log_{10}U_\lambda$. On the other hand, for two curves with the same $\lambda$ but different $\mu$'s the rod curves have approximately the same positions with respect to the axis of $\log_{10}U_\lambda$ but are relatively displaced parallel to the axis of $\log_{10}W_\mu$.

It follows from these experimental conclusions that the relation between $\log_{10}(U_\lambda)_s$ {$(U_\lambda)_s$ stands for the I.b.i. of the rod system acting alone} and $\log_{10}W_\mu$ must be of the form

$$\log_{10}(U_\lambda)_s + \log_{10}s_\lambda = F(\log_{10}W_\mu + \log_{10}S_\mu),$$

(2)

where $s_\lambda$ depends only on $\lambda$, $S_\mu$ depends only on $\mu$ and $F(x)$ is a fixed function of $x$ determined by the shape of the rod curve. Relation (2) may be written

$$\log_{10}s_\lambda(U_\lambda)_s = F(\log_{10}W_\mu S_\mu).$$

This implies that $s_\lambda(U_\lambda)_s$ is a fixed function of $S_\mu W_\mu$. It is equally true that $1/s_\lambda(U_\lambda)_s$ is a fixed function of $S_\mu W_\mu$, which we may call $\xi_s(W_\mu S_\mu)$. Thus

$$1/(U_\lambda)_s s_\lambda = \xi_s(W_\mu S_\mu),$$

or

$$1/(U_\lambda)_s = s_\lambda \xi_s(W_\mu S_\mu),$$

(3)

The experimental data determine only the relative values of $s_\lambda$ at different wave-lengths $\lambda$, and the relative values of $S_\mu$ at different wave-lengths $\mu$.

* Including curves for a number of combinations for which the results cannot be given in full.
It is convenient to remove these ambiguities, (a) by giving the fixed function $\xi_s(x)$ the value unity when $x = 0$ so that $s_\lambda$ is the reciprocal of the l.b.i. of the rods when $W_\mu$, the intensity of the central field, is zero and (b) by giving the fixed function $\xi_s(x)$ the value 0.1 when $x = 1$. It follows from condition (b) that if $W_\mu S_\mu = 1$, $\xi_s(W_\mu S_\mu) = 0.1$ and $1/(U_\lambda)_s$ has one-tenth its value for a central field of zero intensity. Thus $S_\mu$ equals the reciprocal of the intensity of the central field necessary to reduce $1/(U_\lambda)_s$ to one-tenth, or to increase $(U_\lambda)_s$ to ten times its value for zero field. In this sense $S_\mu$ measures the sensitivity of the rod system to the “conditioning” effect of central fields of different wave-lengths.

It is easily deduced from equation (3) that the curve of $(-\log_{10}\xi_s(x))$ against $\log_{10}x$ must have the same shape as the rod section of any experimental curve of $\log_{10}U_\lambda$ against $\log_{10}W_\mu$. The plot of $(-\log_{10}\xi_s(x))$ against $\log_{10}x$ shown as curve 1 in fig. 36 is simply the rod section of curves I and II of fig. 22 placed in such a position with respect to the axes that the two conditions $\xi_s(x) = 1$ when $x = 0$ and $\xi_s(x) = 0.1$ when $x = 1$ are satisfied. Thus curve 1 of fig. 36 completely defines the fixed function of the rods, $\xi_s(x)$.

The curve of $\log_{10}s_\lambda$ against $\lambda$ will coincide approximately with the parafoveal curve of $\log_{10}(1/U_\lambda)$ against $\lambda$ for zero field (fig. 11), except in the red end of the spectrum where $\log_{10}s_\lambda$ will have slightly lower values owing to the participation of the cones in determining $U_\lambda$. The mean values of $\log_{10}S_\mu$ obtained from the rod sections of the various experimental curves of $\log_{10}U_\lambda$ against $\log_{10}W_\mu$ are given in Table II. The variation of $\log_{10}S_\mu$ with $\mu$ is very similar to the variation of $\log_{10}s_\lambda$ with $\lambda$, as is shown by the approximate constancy of $\log_{10}s_\lambda - \log_{10}S_\mu$, $(\lambda = \mu)$.

### Table II

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<td>7.1</td>
<td>6.4</td>
<td>4.1</td>
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<td>1.1</td>
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This means that to a first approximation the relative values of lights of different wave-length in producing a threshold stimulation of the rods and in bringing the rods to a given level of stimulation are the same.

The above discussion applies in the first instance to the response of the rods to test stimuli entering centrally. To allow for entry at other points, the factor $10^{-p_\lambda(d-d_m)^2}$ may be introduced in the expression for $1/(U_\lambda)_s$ which now becomes

$$1/(U_\lambda)_s = 10^{-p_\lambda(d-d_m)^2}s_\lambda\xi_s(W_\mu S_\mu),$$ (4)
where $p_{\lambda \beta}$ determines the directional effect of the rods. For $\lambda$ not greater than 600 m$\mu$ we may identify $p_{\lambda \beta}$ with the $p_{\lambda}$ plotted in fig. 7. For longer wave-lengths $p_{\lambda \beta}$ may be less than $p_{\lambda}$.

Turning now to the cones, we consider the possibility that the l.b.i. of the cones $(U_{\lambda})_{\mu}$ can be represented by an expression similar in form to that already obtained for the rods. For the combination $\lambda = 580, \mu = 500$ (fig. 19), the cone section of curve I extends from the highest brightness levels down to a brightness ($\log_{10} W_\mu = 6.2$ approx.) where the curve becomes nearly horizontal and the l.b.i. of the cones has become constant. We may take a tracing of this pure cone curve and try to fit it over the cone sections of the curves for other combinations $\lambda, \mu$, which have an identifiable cone section. The process is much less satisfactory than in the case of the rods, partly because for most of the available curves the mixed section of the curve where both rods and cones are operative intervenes before the flat part of the cone curve is reached.

A more radical difficulty is revealed by the measurements for the combination $\lambda = 500, \mu = 580$ (fig. 23). The curves of $\log_{10} U_\lambda$ against $\log_{10} W_\mu$ show a sharp "change of law" when $\log_{10} W_\mu$ is in the neighbourhood of 2 and at about the same brightness $p_{\lambda}$ rises sharply. As before we attribute these features to a transition from rod to cone vision of the test stimulus. Comparing curves I and II of fig. 23 with the corresponding curves of fig. 15 for which $\mu$ has the same value (580 m$\mu$), it is easy to see that the cone sections for the two cases cannot arise from a curve of fixed shape which is merely displaced parallel to the axis of $\log_{10} U_\lambda$ by varying amounts depending on the value of $\lambda$. If this were so the gradients of the cone sections in figs. 23 and 15 at a given value of $\log_{10} W_\mu$ would be the same, for these gradients are unaffected by displacements parallel to the axis of $\log_{10} U_\lambda$. Actually at $\log_{10} W_\mu = 2.6$, the gradient (tangent) of curve I equals 0.2 in fig. 23 and 1.0 in fig. 15. Similarly, if we compare the cone sections of fig. 23 with those of fig. 14 for which $\lambda$ has the same value, it is clear that the cone sections for the two cases cannot arise from a curve of fixed shape which is merely displaced parallel to the axis of $\log_{10} W_\mu$ by varying amounts depending on the value of $\mu$.

It must be concluded from the above that the cone curves for different combinations $\lambda, \mu$ cannot be represented by an expression similar to (4). Other anomalies in the cone curves confirm this conclusion. Thus the simple idea of a curve of fixed shape which is displaced parallel to the axes of $\log_{10} U_\lambda$ and $\log_{10} W_\mu$ by amounts depending on the values of $\lambda$ and $\mu$ respectively, breaks down for cone vision although it holds for rod vision. The more complex behaviour of the parafoveal cones is elucidated by the
measurements for foveal vision of the stimulus which give the response of a cone system unobscured by the presence of a rod response. It appears that to explain the response of the cones the duplicity theory must be supplemented with the idea of three distinctive types of cone, an idea which is, of course, inherent in many forms of the trichromatic theory.

8. CENTRAL FIELD ILLUMINATED: FOVEA

When the eye is adapted to a field of zero brightness, the fovea exhibits a pronounced directional sensitivity for all wave-lengths of the test stimulus. Measurements made with the central field illuminated show that this pronounced directional sensitivity is retained whatever the intensity and wave-length of the central field. These measurements consisted in the main of two-point determinations in which \( \lambda \) and \( \mu \) were kept constant while the energy intensity of the central field \( W_{\mu} \) was increased in steps from zero upwards. The determination of \( \log_{10} U_{\lambda} \) for "central" entry of the test stimulus was made at \( d_{o} = + \frac{3}{2} \) or +1 mm. (temporal) as it was known that for the fovea of this eye \( d_{m} \) equalled about 0.9 mm. The determination for peripheral entry was made, in most cases, at \( d_{p} = -3 \) mm. (nasal). Except where the contrary is indicated, the rays forming the central field entered the eye through the centre of the pupil, i.e. at \( d = 0 \). An adequate period of dark-adaptation preceded the run. A few minutes' adaptation to the higher brightness levels was necessary before steady values could be obtained.

The results obtained when the test stimulus and central field had the same wave-length are plotted in figs. 24–27. For \( \lambda = \mu = 580 \) m\( \mu \), \( p_{\lambda} \) remains practically constant at all brightness levels. For the other wave-lengths there is some variation in \( p_{\lambda} \) which can be followed despite the scatter of the experimental points. The curves relating \( \log_{10} U_{\lambda} \) and \( \log_{10} W_{\mu} \) for wave-lengths 500, 580 and 690 m\( \mu \) are of nearly the same shape, that is to say, they can be obtained by moving a single curve without rotation to different positions with respect to the axes. The curves for the wave-length 430 m\( \mu \), however, show a significant difference in shape from the others. Thus even in the restricted case when test stimulus and central field have the same wave-length, the notion of a curve of fixed shape which is merely displaced to different positions with respect to the axes breaks down.

Figs. 28–35 give the results for eight combinations in which the wave-length of the test stimulus lies in the range 430 to 500 m\( \mu \) while \( \mu \), the wave-length of the central field, is considerably greater than \( \lambda \) and lies in
the range 500 to 590 m\(\mu\). For every combination except \(\lambda = 430, \mu = 500\), the curves of \(\log_{10} U_\lambda\) against \(\log_{10} W_\mu\) show a "change of law" of the kind already met with for parafoveal vision, and \(p_\lambda\) shows a corresponding increase from an approximately constant value in a range of low brightnesses to an approximately constant but different value in a range of high brightnesses.

These features of the results can be explained by assuming that there are two types of cone in operation, each with distinctive properties. In fig. 31a* (p. 95), for example, we assume that the left-hand section of curve I, extrapolated as a broken line to higher values of \(\log_{10} W_\mu\), is the curve connecting \(\log_{10} U_\lambda\) with \(\log_{10} W_\mu\) which would be obtained if cones of one type (type X) were acting alone. Similarly we assume that the right-hand section of curve I, extrapolated as a dotted line, is the curve which would be obtained if cones of the other type (type B) were acting alone. These component curves will lead to the observed curve when both types are in action if the observed l.b.i. coincides approximately with the smaller of the l.b.i.'s of the two types except where these have equal or nearly equal values.

Curve II is obtained by displacing the two component curves of curve I without rotation in a direction parallel to the axis of \(\log_{10} U_\lambda\). The component curve of type B must be displaced by a greater amount than that of type X. This connexion between curves I and II is explained if the directional sensitivity of each type of cone is independent of brightness level and type B has a greater directional sensitivity than type X.

A similar explanation may be given of the results for the other combinations in this group if we admit that as \(\lambda\) decreases the vertical separation of the \(X\) and \(B\) component curves diminishes until for \(\lambda = 430 m\mu\) (fig. 35) the \(X\) curve lies above the \(B\) curve at all values of \(\log_{10} W_\mu\) and plays little if any part in determining the resultant curve. For \(\lambda = 490, \mu = 590\) (fig. 29), curves I and II show a new feature. The \(B\) component curves become suddenly horizontal at \(\log_{10} W_\mu = 1.1\) approx. There is an indication of a similar effect for the combination \(\lambda = 500, \mu = 580\) (fig. 28). This effect might be attributed to a third type of cone but as shown below such an explanation is unlikely. It appears instead that for certain wave-lengths \(\mu\), the conditioning effect of the central field on the \(B\) cones is limited, that is to say, however great the intensity of the central field it cannot increase the l.b.i. of the \(B\) cones above a certain value.

Setting aside the anomaly just noted, it is found that those sections of the experimental curves which are identified with the \(X\) or \(B\) component curves can all be fitted approximately with a curve of fixed shape (curve 2

\* The experimental data in this figure are the same as in fig. 31.
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Figs. 24–27. Key as for figs. 14–16.
of fig. 36) which is moved (without rotation) to different positions with respect to the axes.

A series of twenty-one runs was then made with a test stimulus of wavelength 480 m\(\mu\) and with central fields of wave-lengths ranging from 430 to 700 m\(\mu\). The l.b.i. was determined only for central entry of the test stimulus. The rays forming the central field entered the eye through the same point as the rays forming the test stimulus. Some of the results obtained are plotted in fig. 37. The vertical scale of fig. 37 is correct for all the data, but the horizontal scale is correct only for \(\mu = 700\) m\(\mu\). For other values of \(\mu\) the origin of the horizontal scale has been shifted by arbitrary amounts to give a convenient spacing of the curves. For all wave-lengths of the central field except 430 and 480 m\(\mu\), the experimental results can be represented approximately by the two curves shown, which are reproductions of curve 2 of fig. 36. Moreover, the upper of the two curves, which is associated with the \(B\) cones, flattens out at approximately the same value of \(\log_{10} U\lambda\) (5.5) for all values of \(\mu\). The lower curves, which are associated with the \(X\) cones, also flatten out at a common value, about 6.8 in this case. This is to be expected, however, since with a central field of zero intensity \((\log_{10} W\mu = -\infty), \log_{10} U\lambda\) must be the same whatever the value of \(\mu\).* The horizontal separation of the \(B\) and \(X\) curves decreases as \(\mu\) decreases below about 560 m\(\mu\) until at \(\mu = 480\) m\(\mu\) the two curves no longer intersect and the results are represented by the \(X\) curve only. The limited conditioning of the \(B\) cones at high brightnesses is in evidence for \(\mu = 580\) and 610 m\(\mu\), but not for \(\mu = 560\) m\(\mu\) or less. It is not observable for \(\mu = 640\) or 700 m\(\mu\), but this may be because the brightness of the central field could not be made sufficiently high for these wave-lengths.

A selection from a similar set of nineteen runs with \(\lambda = 430\) m\(\mu\) and with \(\mu\) varying from 640 to 410 m\(\mu\) is shown in fig. 38. For \(\mu\) greater than 460 m\(\mu\) a single curve of the form of curve 2, fig. 36, can be drawn to represent the results apart from the limited conditioning effect which occurs for \(\mu = 580\) and 620 m\(\mu\). For \(\mu\) equal to 460 m\(\mu\) or less two curves of the standard shape are required as shown. The two curves intersect before the upper curve has flattened out, but since the shape of the curves is fixed it can still be deduced that the upper curve would flatten out to about the same value of \(\log_{10} U\lambda\) (5.5) in each case.

In a third series of eleven runs, the wave-length of the central field was equal to 600 m\(\mu\) in every case and the wave-length of the test stimulus was varied from 410 to 510 m\(\mu\) (fig. 39). In the figure, the horizontal scale is correct for all combinations \(\lambda, \mu\). The vertical scale is correct only for

* Apart from day-to-day variations in the sensitivity of the eye.
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Figs. 28–35. Key as for figs. 14–16.
\( \lambda = 510, \mu = 600 \) and is displaced by arbitrary amounts for the other cases. For \( \lambda = 510, \mu = 600 \), the upper and lower curves are associated with the \( B \) and \( X \) cones respectively. As \( \lambda \) decreases, the component curves maintain their positions with respect to the horizontal axis but they are displaced by different amounts parallel to the vertical axis. For \( \lambda = 410 \) and 430 m\( \mu \), the results are represented approximately by the \( B \) curve only. In every case the \( B \) curve becomes abruptly horizontal at \( \log_{10} \mu = 1.2 \) approx. Thus, whatever the wave-length of the test stimulus, a central field of wave-length 600 m\( \mu \) has a limited conditioning effect on the \( B \) cones and can raise the l.b.i. of the \( B \) cones to about 4-3 times the value for zero field but no more. Taking account of all the data obtained, it appears probable that the same thing is true for a central field of any wave-length exceeding 570 m\( \mu \) although insufficient intensity of the central field prevents our observing the effect for \( \mu = 640 \) m\( \mu \) or more.

The above results show that the l.b.i. of the \( B \) cones acting alone \((U_\lambda)_b\) can be represented approximately by the following expression, which is similar to that used for the rods,

\[
\frac{1}{(U_\lambda)_b} = b_\lambda \xi(\frac{W_\mu B_\mu}{\mu}) 10^{-p_\lambda(d-d_m)^2},
\]

where \( b_\lambda \) is independent of \( \mu \) and equals the reciprocal of the l.b.i. of the \( B \) cones when the central field has zero energy,

\( B_\mu \) is independent of \( \lambda \) and equals the reciprocal of the energy of the central field necessary to raise the l.b.i. of the \( B \) cones to ten times the value for zero field,

\( \xi(x) \) is a fixed function of \( x \). Curve 2 of fig. 36 gives a plot of \( \{-\log_{10}\xi(x)\} \) against \( \log_{10}x \),

\( p_{Ab} \) determines the directional sensitivity of the \( B \) cones for a test stimulus of wave-length \( \lambda \).

For wave-lengths of the central field greater than 570 m\( \mu \), the modified form of \( \xi(x) \) shown as curve 3 in fig. 36 must be used to allow for the limited conditioning effect obtained with these wave-lengths. In such cases \( B_\mu \) is defined as “the reciprocal of the energy of the central field which would raise the l.b.i. of the \( B \) cones to ten times the value for zero field if the limited conditioning effect did not operate”.

We may adopt an analogous expression for the l.b.i. of the \( X \) cones acting alone, \((U_\lambda)_x\). We put

\[
\frac{1}{(U_\lambda)_x} = x_\lambda \xi(\frac{W_\mu X_\mu}{\mu}) 10^{-p_\lambda x(d-d_m)^2},
\]

where \( x_\lambda, X_\mu, p_{Ax} \) are defined in precisely the same way as \( b_\lambda, B_\mu \) and \( p_{Ab} \).
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**Fig. 31a**

- FOVEA
  - $\lambda = 470 \text{ m}\mu$
  - $\mu = 560 \text{ m}\mu$

**Fig. 36.** The rod function $\xi_s(x)$, the cone function $\xi(x)$, and the modified cone function $\xi'(x)$ applicable to the blue cones when $\mu$ exceeds 570 m$\mu$. 
respectively. \( \xi(x) \) is, to a sufficient approximation, the same function as for the \( B \) cones. No limited conditioning effect has been observed for the \( X \) cones.

From a curve such as curve I of fig. 31a where the \( X \) and \( B \) components are well defined the values of \( b_\lambda, B_\mu, x_\lambda \) and \( X_\mu \) are easily obtained in the way illustrated in the figure. For other cases the process is less certain. The mean results of all the determinations of \( b_\lambda, x_\lambda, B_\mu \) and \( X_\mu \) (for \( \lambda \) less than 520 m\( \mu \)) are plotted in figs. 40 and 41. The curve of \( \log_{10} b_\lambda \) against \( \lambda \) (curve 1, fig. 40) has a maximum at \( \lambda = 440 \) m\( \mu \) approximately, which means that the \( B \) cones, or the blue cones as we may now call them, are most sensitive to test stimuli of wave-length 440 m\( \mu \). Owing to the limited conditioning effect the l.b.i. of the blue cones has a maximum value \( M_\lambda \) for central fields of wave-length \( \mu \) greater than 570 m\( \mu \). Curve 2 of fig. 40 shows the observed variation of \( \log_{10} 1/M_\lambda \) with \( \lambda \). Curve 2 is obtainable from curve 1 by a simple vertical displacement. Thus, if what we have called the limited conditioning effect were due to a third type of cone, the relative spectral sensitivity to test stimuli of different wave-length would be the same as for the blue cones.

The curve of \( \log_{10} B_\mu \) against \( \mu \) (curve 1, fig. 41), shows that the conditioning effect of the central field on the blue cones is greatest for \( \mu = 445 \) m\( \mu \) approx. The sensitivity curves of the blue cones to test stimuli of different wave-length (curve 1, fig. 40) and to central fields of different wave-length (curve 1, fig. 41) appear to be slightly different in shape in the region of the spectrum (410–510 m\( \mu \)) where both can be followed although the difference may be experimental error. As \( \mu \) increases beyond 510 m\( \mu \) the curve of \( \log_{10} B_\mu \) descends steadily until at \( \mu = 570 \) m\( \mu \) it swings round and becomes horizontal to descend again steadily for \( \mu \) greater than 600 m\( \mu \). This change of form at \( \mu = 570 \) m\( \mu \) may be connected with the limited conditioning effect of central fields for which \( \mu \) exceeds 570 m\( \mu \). If the limiting conditioning effect were due to a third type of cone, the appropriate sensitivity curve to central fields of different wave-length would have to exhibit something like a discontinuity in the neighbourhood of \( \mu = 570 \) m\( \mu \). The simpler view and the one adopted here is that we are dealing with a special property of the blue cones.

We are naturally led to consider whether two types of cone are sufficient to explain all measurements of the present type. Fig. 39 shows that as \( \lambda \) increases the vertical separation of the \( B \) and \( X \) component curves increases until at \( \lambda = 510 \) m\( \mu \) the \( B \) component is responsible only for the upper extremity of the experimental curve. We may anticipate that for still greater values of \( \lambda \) (540 m\( \mu \) or more) the process will be continued and the
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Fig. 37. Curves of \( \log_{10} U_\lambda \) v. \( \log_{10} W_\lambda \) for \( \lambda = 480 \) m\( \mu \) and different values of \( \mu \). (The curves are displaced by arbitrary amounts parallel to the axis of \( \log_{10} W_\lambda \) to give a convenient spacing.)

Fig. 38. Similar to fig. 37 but for \( \lambda = 430 \) m\( \mu \).

Fig. 39. Curves of \( \log_{10} U_\lambda \) v. \( \log_{10} W_\lambda \) for \( \mu = 650 \) m\( \mu \) and for different values of \( \lambda \). (Curves displaced by arbitrary amounts parallel to the axis of \( \log_{10} U_\lambda \) to give a convenient spacing.)

Fig. 42. Key as for figs. 14–16.

Fig. 43. For key see p. 100 of text.
experimental curve will consist simply of the X component. measurements show, however, that with test stimuli of wave-length greater than 540 mμ the relation between log₁₀ Uλ and log₁₀ Wμ cannot be represented by the standard curve (curve 2, fig. 36) for all wave-lengths of the central field. In some cases, such as that shown in fig. 42, a change of law of the familiar kind is in evidence. Thus the X cone system is not a simple system. One possibility is that two cone systems, which we may call the green and red systems, are in operation, whose l.b.i.'s are represented by the expressions:

\[
1/(U_\lambda) = g_\lambda \xi(W_\mu G_\mu) 10^{-p_{\lambda g}(d-d_m)^2}, \quad (7)
\]

\[
1/(U_\lambda) = r_\lambda \xi(W_\mu R_\mu) 10^{-p_{\lambda r}(d-d_m)^2}, \quad (8)
\]

where \(g_\lambda, G_\mu, p_{\lambda g}\) and \(r_\lambda, R_\mu\) and \(p_{\lambda r}\) have similar definitions to those given for \(b_\lambda, B_\mu\) and \(p_{\lambda b}\). The above expressions would then take the place of the single expression (6) for the X cones. Many more measurements will be required for the full working out of this view since it appears that the spectral sensitivities of the red and green systems do not differ so radically as do those of the blue and X systems. From the results so far obtained it is probable that for test stimuli of wave-length not greater than 510 mμ, the X component curve differs little from the curve of one of the two systems introduced above. Thus the values of log₁₀ x_λ and log₁₀ X_μ plotted in figs. 40 and 41 may be identified with log₁₀ g_λ and log₁₀ G_μ respectively. Using the data of fig. 42 and other similar data a first attempt can be made to construct the sensitivity curves of the green and red cones. The curves so obtained are shown as broken lines in figs. 40 and 41. In fig. 41, the three lower curves give the values obtained for \(p_{\lambda b}, p_{\lambda g}\) and \(p_{\lambda r}\) which measure the directional sensitivities of the blue, green and red cones. The difference between \(p_{\lambda b}\) and \(p_{\lambda g}\) for \(\lambda\) less than 500 mμ is well established. The crossing of the curves for \(p_{\lambda g}\) and \(p_{\lambda r}\) at \(\lambda = 620\) mμ is less certain. In figs. 40 and 41 all curves or parts of curves shown by broken lines must be regarded as tentative only.

A striking difference in properties between the blue cones and the red or green cones is indicated if we compare the sensitivity to a test stimulus of given wave-length with the sensitivity to the conditioning effect of a central field of the same wave-length. This comparison may be made by taking the differences log₁₀ \(b_\lambda - b_\mu\), log₁₀ \(B_\mu\), log₁₀ \(g_\lambda - G_\mu\) and log₁₀ \(r_\lambda - R_\mu\) for \(\lambda = \mu\). log₁₀ \(b_\lambda - b_\mu\) is of the order of 2-0 whereas log₁₀ \(g_\lambda - G_\mu\) for

* This conclusion assumes that the sensitivity curves of the B and X components to test stimuli of different wave-length (curves 1 and 3 of fig. 40) will have approximately the same shape as the corresponding sensitivity curves to central fields of different wave-length (curves 1 and 2 of fig. 41) which can be followed throughout the spectrum.
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and \( \log_{10} r_\lambda - \log_{10} R_\mu \) equal about 2·7 and 2·8 respectively. The meaning of this result is apparent if we note that the fixed function \( \xi(x) \) approximates to \( 0.11/x \) for sufficiently high values of \( x \). Thus for central fields of sufficiently high brightness and for central entry of the test stimulus:

\[
1/(U_{\lambda})_b = b_\lambda \xi(W_\mu/B_\mu) = b_\lambda 0.11/W_\mu B_\mu
\]

or

\[
(U_{\lambda})_b/W_\mu = B_\mu/0.11b_\lambda.
\] (9)

Now when \( \lambda = \mu \), \( (U_{\lambda})_b/W_\mu \) represents in a certain sense the Fechner fraction of the blue\(^1\) cones acting alone. Similarly, \( (U_{\lambda})_g/W_\mu = G_\mu/0.11G_\lambda \) and \( (U_{\lambda})_r/W_\mu = R_\mu/0.11r_\lambda \) represent respectively the Fechner fractions of the green and red systems acting alone. Thus the fact that \( \log_{10} B_\mu - \log_{10} b_\lambda \) or \( \log_{10} B_\mu/b_\lambda \) exceeds \( \log_{10} G_\mu - \log_{10} g_\lambda \) or \( \log_{10} G_\mu/g_\lambda \) by approximately 0·7 means that the limiting Fechner fraction of the blue cones at high brightnesses is about five times that of the green cones.

Reverting for a moment to the rods, Table II shows that for \( \lambda = \mu \), \( (U_{\lambda})_b/W_\mu \) equals about 1·0. Comparison with the cones is complicated by the difference in shape of the rod and cone functions (curves 1 and 2 of fig. 36). It can be deduced, however, that the Fechner fraction of the rods at high adapting brightnesses lies between 3 and 10 times the limiting Fechner fraction of the blue cones.

A brief reference must be made to the changes in the apparent colour of the test stimulus, when its intensity is just above the threshold, which are observed as the brightness of the central field is increased. In cases similar to that of fig. 31, there occurs a change in colour which corresponds broadly to the change in law of the experimental curve of \( \log_{10} U_\lambda \) against \( \log_{10} W_\mu \). In other cases where test stimulus and central field have the same wavelength, the test stimulus appears as a white flash.

9. Change in the point of entry of the rays forming the central field. Foveal vision

When the rays forming the central field are sent into the eye near the periphery of the pupil instead of at or near the centre, measurements of the l.b.i. for different points of entry of the test stimulus give a curve of \( \log_{10} U_\lambda \) against \( d \) of the same general shape as before. The main difference is that the absolute values of \( \log_{10} U_\lambda \) are in general smaller for peripheral than for central entry of a central field of fixed energy. This means that the
effectiveness of the central field in raising the l.b.i. above the value for zero field depends on the direction of incidence on the retina of the rays forming the central field. The magnitude of the directional effect for the central field is of the same order as that for the test stimulus. It is possible, however, that the curve of \( \log_{10} U_\lambda \) against \( d \) may not be of quite the same shape for different points of entry of the central field. A difference was observed in one set of measurements, but has not yet been confirmed.

The two sets of data of fig. 43 show the variation of \( \log_{10} W_\mu \) with \( \log_{10} W_\mu \) (\( \lambda = 480, \mu = 580 \)) for a test stimulus entering at \( d = +1 \) (temp.) and for a central field entering at \( +1 \) (temp.) (circle points) or \( -2\frac{1}{2} \) (nal) (cross-points). To a first approximation each curve can be resolved into two component curves, corresponding to the blue and the green cones respectively, and the effect of changing the point of entry of the central field appears as a displacement of each component curve parallel to the axis of \( \log_{10} W_\mu \). Similar results were obtained for the combination (\( \lambda = 480, \mu = 600 \)). The horizontal displacement of each component curve determines the directional sensitivity of the corresponding type of cone to the conditioning effect of the central field just as the vertical separation of each component curve in fig. 31 determines the directional sensitivity to the test stimulus. It should be possible by this method to measure the directional sensitivity of the blue, green and red cones to the conditioning stimulation over the same range of values of \( \mu \) for which \( B_\mu, G_\mu \) and \( R_\mu \) can be determined (see fig. 41).

When the point of entry of the central field is allowed to vary the expressions given above for \( 1/(U_\lambda)_b \), \( 1/(U_\lambda)_g \) and \( 1/(U_\lambda)_r \) must be modified. As a tentative suggestion we may put

\[
1/(U_\lambda)_b = b_\lambda 10^{-p_\lambda (d-d_m)^2/2} \exp\{W_\mu B_\mu 10^{-p_\mu (d'-d_m)^2/2}\},
\]

and similar expressions for \( 1/(U_\lambda)_g \) and \( 1/(U_\lambda)_r \), where \( d' \) is the point of entry of the central field and \( P_\mu \) determines the directional sensitivity of the blue cones to a conditioning stimulation of wave-length \( \mu \). This form assumes that the curve of \( \log_{10} U_\lambda \) against \( d \) has the same shape for all points of entry of the central field.

10. General Discussion

Fig. 44 summarizes in a single diagram the connexion between the sensitivity and the condition of stimulation of the foveal retina to which we are led by the present work. We imagine that the eye views the \( 10^\circ \) patch of
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Fig. 40. Variation with $\lambda$ of $\log_{10}b_\lambda$, $\log_{10}^2\lambda$ (or $\log_{10}^2\theta_\lambda$), $\log_{10}r_\lambda$, $\log_{10}(1/M_\lambda)$, $P_{\lambda b}$, $P_{\lambda g}$ and $P_{\lambda r}$.

Fig. 41

Fig. 44. Diagram showing how the experimental curve of $\log_{10}U_\lambda$ against $\log_{10}W_\mu$ for any combination $\lambda, \mu$ is derived from three component curves appropriate to the three types of cone. Foveal vision.
light of wave-length \( \mu \) and energy \( W_{\mu} \) and that we determine the l.b.i. \( U_\lambda \), for a monochromatic test stimulus of wave-length \( \lambda \) at different energies \( W_{\mu} \) from zero upwards. Our view is that there are three types of cone in operation, each one of which in the absence of the others would give a curve of \( \log_{10} U_\lambda \) against \( \log_{10} W_{\mu} \) similar in shape to curve 2 of fig. 36. In the top right-hand quadrant of fig. 44 the three curves \( R \), \( G \) and \( B \) represent the variation of \( \log_{10} U_\lambda \) with \( \log_{10} W_{\mu} \) for the red, green and blue cones respectively, acting alone. The position of each curve with respect to the axes of \( \log_{10} U_\lambda \) and \( \log_{10} W_{\mu} \) is determined by the wave-lengths \( \lambda \) and \( \mu \).

When \( W_{\mu} \) becomes very small and \( \log_{10} W_{\mu} \) tends to minus infinity, each of the three curves flattens out and \( \log_{10} U_\lambda \) becomes constant. This constant value corresponds to the absolute threshold of the particular type of cone and depends only on the wave-length of the test stimulus. We have defined \( b_\lambda \) to be the reciprocal of the absolute threshold of the blue cones for a test stimulus of wave-length \( \lambda \), so that curve \( B \) must flatten out to the value \( \log_{10}(1/b_\lambda) \) or \( \{-\log_{10} b_\lambda\} \). Similarly, curves \( R \) and \( G \) must flatten out to \( \{-\log_{10} r_\lambda\} \) and \( \{-\log_{10} g_\lambda\} \) respectively. In the top left-hand quadrant of fig. 44, \( \{\log_{10} b_\lambda\}, \{-\log_{10} g_\lambda\} \) and \( \{-\log_{10} (r_\lambda)\} \) are plotted against \( \lambda \), the vertical scale being precisely the same as the vertical scale of \( \log_{10} U_\lambda \) on the other side of the diagram. The three curves are simply curves 1, 3 and 4 of fig. 40, turned upside down. Thus if we take a particular wave-length of the test stimulus, say \( \lambda = 470 \text{ m} \mu \), then the vertical line through 470 on the axis of \( \lambda \) will intersect the curve of \( \{-\log_{10} g_\lambda\} \) at the value to which curve \( G \) must flatten out when \( \log_{10} W_{\mu} \) tends to minus infinity. The values at which curves \( R \) and \( B \) flatten out are similarly determined.

It remains to fix the position of curves \( R \), \( G \) and \( B \) with respect to the axis of \( \log_{10} W_{\mu} \). It will be recalled that \( R_{\mu} \), was defined as the reciprocal of the energy of the 10° patch necessary to raise the l.b.i. of the red cones to ten times their absolute threshold. That is to say, to cause such an increase the 10° patch must have energy \( W_{\mu} \) such that

\[ \log_{10} W_{\mu} = \log_{10}(1/R_{\mu}) = \{-\log_{10} R_{\mu}\}. \]

In the lower right-hand quadrant of fig. 44 \( \{-\log_{10} R_{\mu}\} \) is plotted against \( \mu \), the horizontal scale being precisely the same as the horizontal scale of \( \log_{10} W_{\mu} \) at the top of the figure. Thus if we take a particular wave-length of the 10° patch, say \( \mu = 620 \text{ m} \mu \), the horizontal line through 620 on the axis of \( \mu \) must intersect the curve of \( \{-\log_{10} R_{\mu}\} \) at a point \( P \) whose coordinate on the scale of \( \log_{10} W_{\mu} \) will be the value of \( \log_{10} W_{\mu} \) necessary to raise the l.b.i. of the red cones to ten times their absolute threshold. The point on the curve \( R \) at which the l.b.i. is ten times the absolute threshold is marked
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with a dot \( C \) and the position of curve \( R \) is fixed by bringing this dot to lie on the vertical line through \( P \).

A similar procedure fixes the position of curves \( G \) and \( B \) except that for \( B \) if \( \mu \) exceeds 570 m\( \mu \) the curve must be modified to the form of curve 3 of fig. 36 after its position has been determined by the above method. This modification of curve \( B \) is necessary in the example illustrated in fig. 44.

It is clear that with the aid of the diagram of fig. 44 the three curves \( R, G \) and \( B \) can be drawn in for any wave-lengths of test stimulus and central field.

It has been tacitly assumed that both test stimulus and the conditioning stimulation enter at \( d = d_m \). For other points of entry of the test stimulus the curves \( R, G \) and \( B \) must be shifted upwards parallel to the axis of \( \log_{10} U_\lambda \) by amounts \( p_{\lambda b}(d - d_m)^2 \), \( p_{\lambda g}(d - d_m)^2 \) and \( p_{\lambda r}(d - d_m)^2 \) respectively. For other points of entry of the central field the component curves must be shifted to the right parallel to the axis of \( \log_{10} W_\mu \) by amounts \( p_{\mu b}(d' - d_m)^2 \), \( p_{\mu g}(d' - d_m)^2 \) and \( p_{\mu r}(d' - d_m)^2 \).

The derivation of the resultant curve of \( \log_{10} U_\lambda \) against \( \log_{10} W_\mu \) for foveal vision now depends on a method for determining \( \log_{10} U_\lambda \) at each value of \( \log_{10} W_\mu \) from the values of \( \log_{10}(U_\lambda)_b \), \( \log_{10}(U_\lambda)_g \) and \( \log_{10}(U_\lambda)_r \) given by curves \( B, G \) and \( R \). We have been able to proceed without defining precisely how this is to be done by assuming that \( \log_{10} U_\lambda \) will not exceed the smallest of \( \log_{10}(U_\lambda)_b \), \( \log_{10}(U_\lambda)_g \) and \( \log_{10}(U_\lambda)_r \) and will be actually equal to it except when the smallest and the next smallest have about the same value. Further work on this point is necessary.

For parafoveal vision it has been shown that the rods give rise to a curve of \( \log_{10} U_\lambda \) against \( \log_{10} W_\mu \) which has the shape of curve 1 of fig. 36 and whose position with respect to the axes is fixed, in any given case, by the values of \( \log_{10} S_\lambda \) and \( \log_{10} S_\mu \). The relation between \( \log_{10} U_\lambda \) and \( \log_{10} W_\mu \) given by the parafoveal cones cannot be represented in this simple way. By assuming that the parafoveal cones, like the foveal cones, consist of three species, each with its own spectral sensitivities to test stimulus and conditioning stimulation, we can explain the parafoveal measurements. If the parafoveal and foveal cones had identical properties it would only be necessary to add the rod curve as a fourth component curve in fig. 44 and determine the resultant of the four component curves so obtained. When this is done the resultant curves for different combinations \( \lambda \) and \( \mu \) reproduce the main features of the experimental curves for parafoveal vision, and show anomalies of the kind noted at the end of § 7. However, the agreement in the cone regions of the curves is not quantitative, and we must conclude that there are significant differences in the spectral sensitivities.
of the parafoveal and foveal cones of corresponding type. On the other hand, the shape of the individual cone component curves is probably the same for both parafovea and fovea. Thus, a tracing of curve 2 of fig. 36 can be fitted over the cone sections of curves I and II in fig. 19.

Evidence for the existence of three types of cone and a first crude determination of the unique set of spectral sensitivity curves for these types have been obtained in this investigation by a method completely independent of colour-matching measurements. The precise connexion between the three mechanisms demanded by colour-matching experiments and the three types of cone assumed here must be close but it remains to be elucidated.

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Summary

A light ray terminating on a given point of the retina has different visual effects depending on its direction of incidence on the retina. The direction of incidence can be varied by sending the ray into the eye through different points of the pupil opening. The primary object of this work was to determine the effect of direction of incidence on threshold sensitivity but the results obtained cover the wider problem of the dependence of threshold sensitivity on the condition of stimulation of the retina. The test stimulus was a patch of light of diameter 1° and of wave-length $\lambda$, exposed for a fraction of a second every few seconds. $U_\lambda$, the smallest perceptible intensity of the test stimulus, was measured in energy units, the sensitivity then being defined as $1/U_\lambda$. With parafoveal vision of the test stimulus by the dark-adapted eye it was found that direction of incidence had little effect on sensitivity when $\lambda$ was less than 580 m$\mu$ but a pronounced effect for longer wave-lengths. The dark-adapted fovea gave a pronounced directional effect at all wave-lengths.

The condition of the retina was modified by making the subject view a patch of light of diameter 10° (wave-length $\mu$, and intensity $W$) at whose centre the test stimulus was applied as an additional stimulus. For parafoveal vision, the directional effect showed a marked increase in passing...
The directional sensitivity of the retina

from low to high intensities, and the curve connecting the threshold value $U_A$ and the intensity of the conditioning field $W_\mu$ showed a corresponding change of law. These two connected effects are attributed to a change from rod vision at low intensities to cone vision at high intensities, the rods and cones being assumed to have different directional properties. For foveal vision, which involves the cones only, somewhat similar effects were observed and are explained by assuming three types of cones for which the relative spectral sensitivities are roughly determined. Normally the threshold value increases proportionally with the intensity of the conditioning field at high intensities (Weber's Law) but a striking deviation from this rule was observed for a blue test stimulus on a red conditioning field. Increase in the intensity of the conditioning field beyond a certain value produced no corresponding increase in the threshold value. This result is ascribed to a special property of the "blue" cones. In the present investigation the hypothesis of three types of cone whose properties have been approximately determined has been developed from measurements which are completely independent of colour-matching data.

References

Dziobek 1934 Licht, 4, 150.