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THE ABSOLUTE SENSITIVITY AND FUNCTIONAL STABILITY OF THE HUMAN EYE

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The absolute threshold of the human eye has been measured by a number of workers using a small peripheral test field and a short exposure. Hecht, Shlaer & Pirenne (1942) used a circular test field subtending an angle of 10′ at the eye, placed 20° from a fixation point, and illuminated in 0·001 sec flashes. They found that the average value of the threshold for the dark-adapted periphery corresponds to a flash energy content of about 100 quanta of wave-length 0·51 μ striking the cornea of the eye (54–148 quanta for a 60 % frequency of seeing, depending on the subject). These values correspond to the minimum amount of light energy necessary for vision. Most of the experiments we wish to report here were made under very different conditions, namely using a large test field, about 45° in diameter, exposed to the dark-adapted eye for periods of several seconds without using a fixation point. On account of the large visual angle subtended by the test field and of eye movements, the image is likely to fall in turn on all parts of the retina, including the most sensitive regions of the periphery, during one exposure. When the field is just visible, the total amount of light energy entering the eye during one 5 sec exposure is of the order of 200,000 quanta. This is much greater than in the case of a small flash, but on the other hand the flux of radiating energy reaching the retinal receptors is extremely low. Only a small fraction of the 20 million odd rods covered by the image of the field can possibly absorb a light-quantum during one exposure.

Threshold measurements were made using spectral bands of wave-lengths close to 0·51 μ and isolated by colour filters from the continuous spectrum of an electric tungsten filament lamp. By using other colour filters the scotopic sensitivity curve was measured for two subjects, to check the method. The absolute determinations of radiating energy were based on visual photometric comparisons with electric lamps calibrated for candle-power and colour temperature by the National Physical Laboratory. The threshold was also

determined using the whole white light from the lamp. On the basis of the sensitivity curve, the results were converted into energy values referring to monochromatic light of $\lambda = 0{\cdot}51\,\mu$.

METHODS

The apparatus consisted essentially of a sheet of flashed opal glass lit from behind by a light source and viewed from in front by the subject (Fig. 1). The light sent by the lamp towards the screen could be made to pass through colour filters and neutral wedges. In this way it was possible to control the spectral composition and intensity of the light received by the subject from the screen.

The main advantages of such a source of spectral light are its simplicity of construction and calibration and the fairly large amount of energy it can deliver.

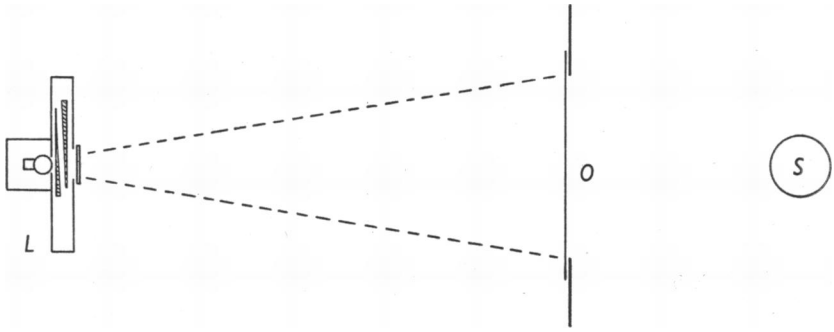

Fig. 1. Diagram giving the plan of the apparatus used for measuring the absolute threshold of the human eye. The subject's head was at *S*. Using ordinary binocular vision, he looked for the test field *O*, made up of a circular sheet of flashed opal glass. When the experimenter opened a shutter (not shown on the figure) the test field *O* was illuminated by the light source *L*. This consisted of an opal electric bulb, the light of which passed through a diaphragm, two adjustable 'neutral' wedges and, generally, a colour filter. A number of screens pierced with suitable holes (not shown) were placed between *L* and *O* in order to cut out stray light.

Light source

A tungsten-filament 12 V 12 W electric lamp with opal bulb was under-run at the accurately controlled voltage of 11·2 V. The electric lamp had been aged by running it at 12 V for 150 hr before any experiments or calibrations were made using it. The current to run the lamp was taken from two 6 V 140 A hr car batteries in series. The electric lamp was contained in a metal box. Light from a portion of the opal lamp was allowed to leave the box through an open diaphragm 19 mm in diameter, the diaphragm being very close to the opal lamp.

The light coming through the diaphragm was made to pass through two neutral wedges. Each wedge could be moved independently upon a rack and pinion, so that any part of it could be placed in front of the opal lamp. The neutral wedges, made by Messrs Ilford Ltd., were of colloidal carbon in gelatine cemented in Canada balsam between two layers of glass. The wedges were each about 25 cm in length and the range of intensities which could be obtained using the two together corresponded to approximately 4·5 logarithmic units (base 10). The position of a wedge could be accurately defined by a reading upon a mm scale mounted on top of the wedge. A 1 mm move-

ment of one wedge corresponded approximately to a 0·01 change in optical density. The optical density D is as usual defined by the equation

$$D = \log_{10} \frac{I}{I_t}, \tag{1}$$

I being the incident light intensity and I_t the intensity transmitted.

A holder for light filters was mounted in front of the neutral wedges so that the light coming from the diaphragmed light source passed through it. In this holder colour filters could be placed.

Special care was taken to make sure that no light could leak around the wedges and their mountings or around the colour filters and the filter holder. If, for example, only $\frac{1}{1000}$th of the light leaving the neutral wedges were to leak around a deep red colour filter this leak might be visually more effective than the light coming through the filter itself. Similarly, if $\frac{1}{1000}$th of the light from the lamp leaked around the neutral wedges this would be more than that coming through the wedges when their combined density was greater than 3. No inconsistencies which could be attributed to such leakages have been observed for the many experiments made upon men and upon animals.

Calibrations

The luminance of an opal glass screen similar to that used in the threshold measurements and lit by the source with neither wedges nor filters in the light beam, was found by the National Physical Laboratory to be 0·0148 equivalent foot-candle when the lamp was 247·4 cm distant from the screen. The screen was viewed from the opposite side to the source.

A periodic check on the intensity of the lamp was made by visual comparison with the light of another lamp, run at a constant voltage but used only for this comparison. During the experiments described here the maximum change was a decrease in brightness of about 2%.

Colour temperature. The relative emissivity of a tungsten lamp run at some given voltage is, for the visible spectrum, almost identical with that of a black-body radiator at some special temperature. If therefore this temperature, the 'colour temperature', is known, the spectral energy distribution of the lamp is known, in arbitrary units, from Planck's equation (Walsh, 1926).

Light from the lamp was photometrically compared with that from a reference lamp calibrated for voltage against colour temperature by the N.P.L. The lamp of the light source (with neither wedges nor filters in front of it) was thus found to have a colour temperature of 2440° K. According to measurements made at the National Physical Laboratory, the colour temperature was reduced by about 40° K after the light had passed through the opal screen. Thus the colour temperature of the light emitted by the screen was 2400° K.

By viewing the photometric field through colour filters it was ascertained that the relative emissivity of the light source lamp (opal bulb) could be made to correspond closely to that of the calibrated lamp (clear bulb) over the visible spectral range. Similarly, although it changed its colour temperature, the opal glass of the screen hardly affected the general black-body character of the light passing through it. The relative spectral energy distribution of the visible light emitted by the opal screen therefore corresponded closely to that of a Planckian radiator of temperature 2400° K.

The calibration of the 'neutral' wedges. The wedges used were not really neutral (Fig. 2). They were calibrated for the spectral bands used in the experiments by a visual photometric method, using rotating sector disks.

The colour filters. The following colour filters were used: Ilford gelatine filters (sealed between glass) nos. 600, 601, 602, 603, 604, 605, 606, 609, Corning glass filter 2408, the combination Corning 2418 and 9780, and the combination Corning 2424, 9830 and 9863 (cf. Fig. 5). The filters were calibrated for transmission by the N.P.L. with a Hardy Recording Spectrophotometer. They seemed to be free from side-bands in the visible spectrum. Several of them transmitted freely in the near infra-red but this is without influence on the present measurements. A number of filters were re-calibrated when the experiments were finished. For some of them no significant change of transmission was found. In other cases small differences were observed. These, however, might perhaps be within the accuracy of the recording spectrophotometer which gives a slightly irregular

line. The greatest difference so found corresponded to 0·03 $\log_{10}$ unit in the value of the total energy η_X transmitted by a given filter (see below under Results, 'The spectral threshold curve').

Measurement of the threshold

The threshold spectral sensitivity curve for two human subjects was measured. The experiment was performed in a dark room, the observer being dark-adapted for 45 min before making observations. The opal glass screen (Fig. 1) was illuminated by the light source placed 105·4 cm from it. The subject viewed the screen from the opposite side to the light source. A black paper cut off all light except a circular disk of diameter 22 cm. The subject's head was not fixed but kept about 30 cm from the centre of the screen. Observations were made using both eyes with natural pupils.

The experimenter changed the filters, adjusted the wedges, turned the light on and off and recorded the results. A 'trial' for a given filter and a given setting of the neutral wedges was made as follows: when the subject was ready, the experimenter opened a shutter and allowed the light source to shine on the opal screen for about 5 sec; he then cut the light off again. When the experimenter turned the light on he said 'on', when he turned it off he said 'off'. The subject reported whether or not he saw the light. The reliability of the subject was checked by putting in 'blanks'; that is, the experimenter gave no light flash, but said 'on' and 'off' as usual. The two subjects in no case said 'seen' after a blank.

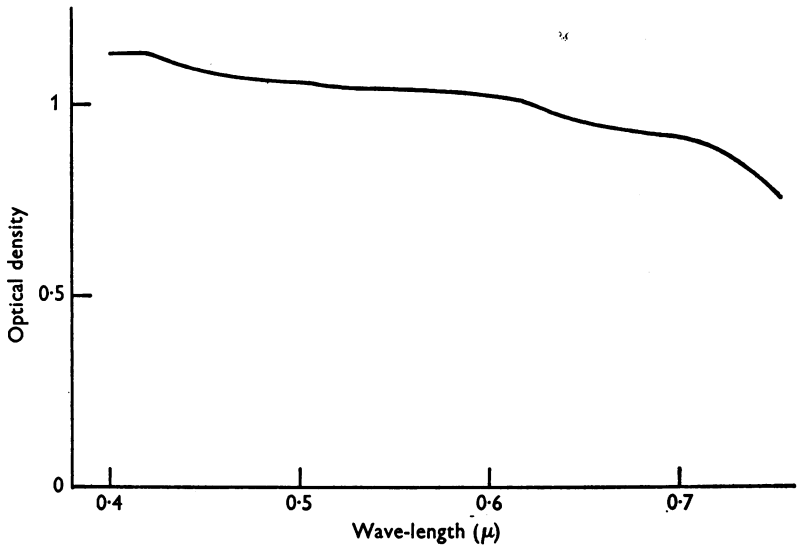

Fig. 2. Spectral density of one of the 'neutral' wedges at a setting 10 cm from its lighter end. The curve is based on measurements made with colour filters and rotating sector disks. These agree with N.P.L. measurements, made with a recording spectrophotometer, of the transmission of a light filter made of the same materials as the wedge.

Preliminary trials were made and the approximate wedge settings for the thresholds of the light transmitted by the filters to be used were found. The threshold for a given filter was finally determined by making, in random order, one trial at each of a number of intensities, 0·1 $\log_{10}$ unit apart and including intensities above and below the threshold intensity.

For any given colour filter, the intensity was varied by changing only the wedge settings. The calibrations of the wedges gave their optical density at any chosen setting, and of course the $\log_{10}$ of the light intensity decreased by 0·1 unit when the total optical density of the wedges increased by 0·1.

RESULTS

Accuracy of the threshold determinations

The thresholds determined by this method were rather sharply defined. In the greater number of cases a change from 'never seen' to 'always seen' occurred for an intensity step of 0·1 $\log_{10}$ unit; that is, the results of these series of trials when re-arranged in order of intensities were of the type

$$0\ 0\ 0\ 0\ +\ +\ +\ +\ +\ +, \qquad \text{(A)}$$

in which 0 means 'not seen' and + means 'seen', the intensity increasing from left to right in steps of 0·1 $\log_{10}$ unit. Series of the following type,

$$0\ 0\ 0\ 0\ +\ 0\ +\ +\ +\ +, \qquad \text{(B)}$$

occurred 2 or 3 times out of 10. More irregular series were very rare.

When the series was regular, the threshold was taken as the $\log_{10}$ intensity midway between the intensities of the last 0 and the first +. When the series was irregular, it was changed for the purpose of calculation into a regular series having the same number of 0 and +, and the threshold value taken as above. This method gives an estimate of the threshold corresponding approximately to a 50% frequency of seeing.

In several random series of trials under the same conditions, the threshold value so estimated rarely changed by more than 0·1 or 0·2 $\log_{10}$ unit. Systematic experiments were made on two subjects to test this repeatability. Ten random series were given in succession, and the frequency of seeing plotted against log. intensity as in Fig. 3. The uncertainty range between none seen out of ten trials and ten seen out of ten is 0·3 $\log_{10}$ unit in one subject and 0·4 in the other. On the basis of these frequency-of-seeing curves it is calculated that the standard error of a threshold value obtained from a single series such as (A) or (B) is about 0·064 $\log_{10}$ unit.

Since it took about 1 hr to make 100 trials, the average interval between trials was approximately $\frac{1}{2}$ min, but for each trial the subject was always allowed to choose the moment when he was ready. It would hardly be possible to make many more trials at one sitting without reaching the onset of fatigue, which would disturb the experiment. The subject was conscious of the fact that in each of these 5 sec trials he was making a number of attempts to decide whether the field was visible or not. He was voluntarily looking in various directions to try and see the test field with the periphery of his retina. Subjectively, a 5 sec trial of this kind involved more mental effort than a trial consisting of a single brief flash with fixation. It will be noted that the frequency-of-seeing curve here is steeper, having an uncertainty range 2 or 3 times smaller than in the latter case.

These observations refer to trained subjects under good experimental conditions. As one would expect, untrained or tired subjects give less regular results and a wider range of uncertainty of seeing (Fig. 4).

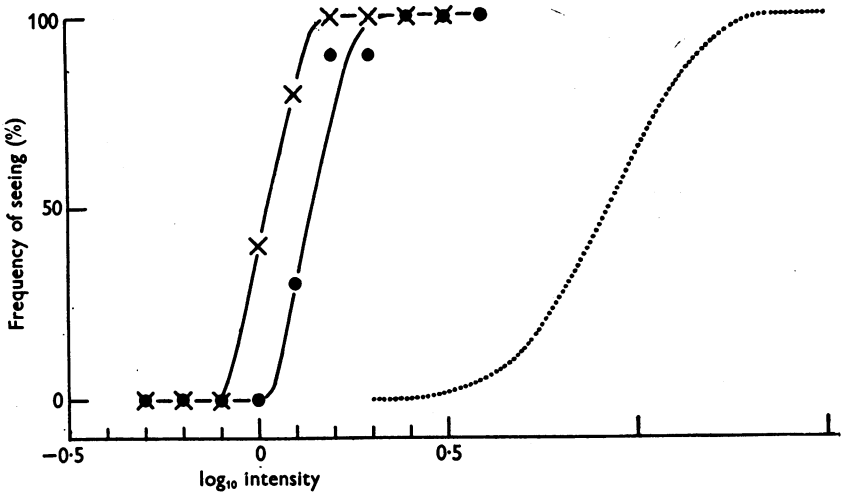

Fig. 3. Curves (full lines) giving the frequency with which the 45° field of Fig. 1, presented binocularly without fixation in 5 sec exposures, was seen at different light intensities by two subjects. Crosses (×) refer to subject M. H. P., black circles (●) to E. J. D. Each experimental point refers to 10 exposures at one given intensity. On the abscissa scale, log. intensity = 0 corresponds to an intensity of $7{\cdot}52 \times 10^{-7}$ erg/sec × steradian × cm^2 (field) for light of wave-length $\lambda = 0{\cdot}51\,\mu$. For purposes of comparison the curve (dotted line) on the right of the figure gives the shape of the Poisson probability integral for a retinal threshold $n = 5$ quanta. This curve is positioned arbitrarily on the log. intensity scale. Frequency-of-seeing curves of similar shape to this theoretical curve were obtained (Hecht *et al.* 1942) for subject M. H. P. using a 10′ test field presented uniocularly 20° from a fixation point in 1 msec flashes. In terms of the total amount of energy entering the eye during one single exposure, the curves representing the latter experiments should be placed on the log. intensity scale about 3 $\log_{10}$ units below the steeper curves (full lines) obtained under the present conditions.

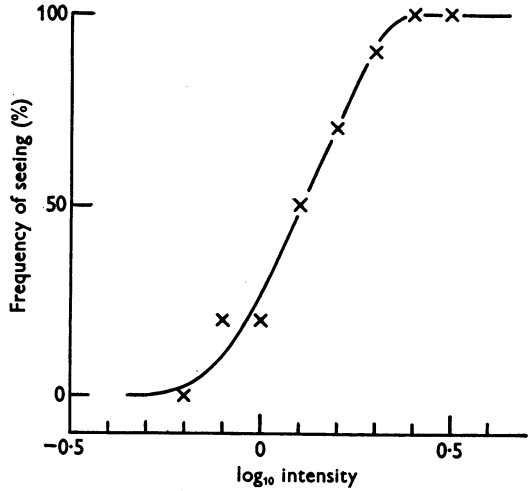

Fig. 4. Frequency-of-seeing curve, obtained under the same conditions as the full-line curves of Fig. 3, but for a subject (M. H. P.) who fell ill with influenza the day after the experiment.

At the threshold intensity determined as above, the subject could just detect the presence of the brighter screen in his visual field. At an intensity twice as high he could distinguish a hand in front of the screen. At an intensity 3 times threshold he could tell when the fingers of the hand were spread out and see the gaps between them.

The test field looked the same to the subjects for all wave-lengths used, and no change in the sharpness of the threshold was observed when the wave-length was changed.

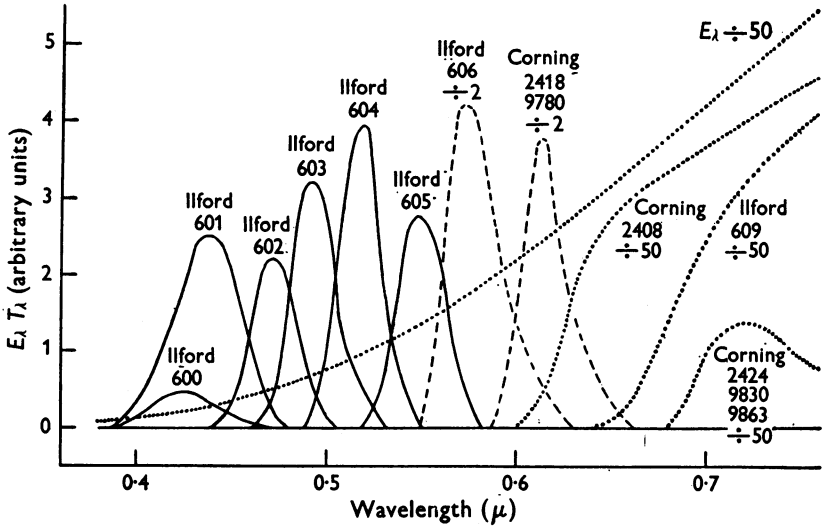

Fig. 5. Relative spectral energy $E_\lambda T_\lambda$ transmitted by the opal screen *O* of Fig. 1 when various colour filters were placed in front of the lamp, the neutral wedges being removed from the light beam. The ordinates of the curves drawn in interrupted lines have been divided by 2, those of the curves in dotted lines by 50. The numbers next to the various curves are those of the corresponding colour filters. The curve E_λ gives the spectral distribution of the light emitted by the opal screen (colour temperature = 2400° K) when no filter was used ($T_\lambda = 1$).

The spectral threshold curve

To plot a first approximation spectral threshold curve, all the energy transmitted by filter X is assumed to be concentrated at a mean wave-length λ_X. The integral

$$\eta_X = \int E_\lambda T_\lambda d\lambda \qquad (2)$$

over the visible spectrum represents the energy in arbitrary units transmitted by the filter, E_λ being the relative energy emitted by the screen, calculated using Planck's equation for 2400° K, and T_λ the transmission (as a fraction) for filter X at wave-length λ. Plots of $E_\lambda T_\lambda$ against λ are shown in Fig. 5. The centre of gravity of the area under the curve of $E_\lambda T_\lambda$ for filter X was taken as determining the mean wave-length λ_X. In the case of the red cut-off

filters a special method was used for the calculation of η_X and λ_X, based on the fact that the longer wave-lengths transmitted contribute but little to the visual effect.

For each colour filter used the total density D_X of the wedges corresponding to threshold was estimated as explained above. The first approximation of the threshold energy H is then given on an arbitrary scale by

$$\log_{10} H = \log_{10} \eta_X - D_X. \quad (3)$$

Fig. 6 represents human threshold values calculated on this basis. Each point represents a particular measurement of $\log_{10} H$. The log. energy scale has been adjusted in Fig. 6 so as to make it zero for the lowest threshold value. There are four series of threshold measurements. The series (+) and (○) were obtained for subject M.H.P. on 2 consecutive days; the average difference between the 2 days is insignificant, being less than 0·02 $\log_{10}$ unit. The series (×) for the same subject had been obtained a year earlier; it is on the average 0·06 $\log_{10}$ unit higher than series (+). Other measurements made using the blue-green filter 604 showed that the threshold for the same subject was liable to vary from day to day within 0·3 $\log_{10}$ unit, that is, a range of 1 to 2. Day-to-day variations of the same magnitude are known from measurements made with flash and fixation in the study of dark-adaptation (Hecht & Mandelbaum, 1939). The absolute measurements of Hecht *et al.* (1942) also showed similar threshold changes. All these variations refer to the intensity measured at the cornea.

The measurements for subject E. J. D. (●) are on the average about 0·15 $\log_{10}$ unit higher than measurements (+) for M. H. P.

Fig. 7 represents a curve (dotted line) drawn through the means of the threshold values for each filter given in Fig. 6. A second, and final, approximation of the threshold curve was calculated in the usual manner (crosses). The experimental points may be affected by errors in the individual threshold determinations and in the calibrations of the apparatus, the compound value of which appears to be roughly $\pm 0{\cdot}20$ $\log_{10}$ unit. This is indicated on Fig. 7. This figure shows that the scotopic sensitivity curve (full line) adopted by the Commission Internationale de l'Éclairage (International Commission on Illumination, 1951) can be fitted to the second approximation within the limits of errors. The C.I.E. curve is based on the results obtained by Crawford (1949) for fifty subjects and on those obtained by Wald (1945) for two groups of subjects, one containing twenty-two members, the other fifty-two.

Absolute energy levels

We wish to calculate in absolute energy units the threshold for blue-green light of $\lambda = 0{\cdot}51\,\mu$, to which the eye is most sensitive—which will of course set the whole spectral threshold curve on an absolute basis. In order to do so, we

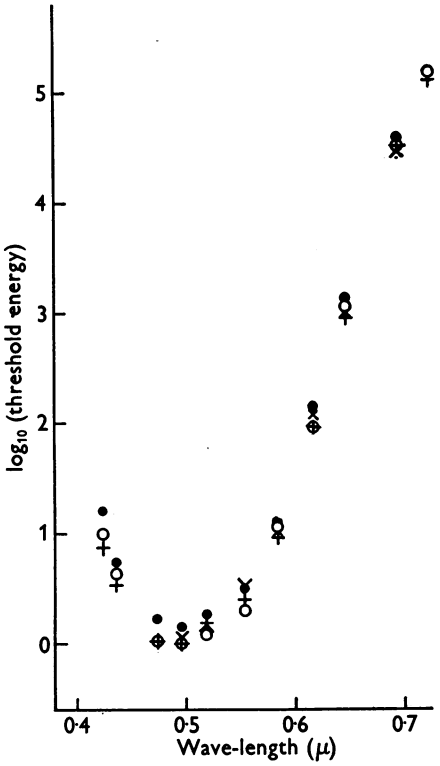

Fig. 6

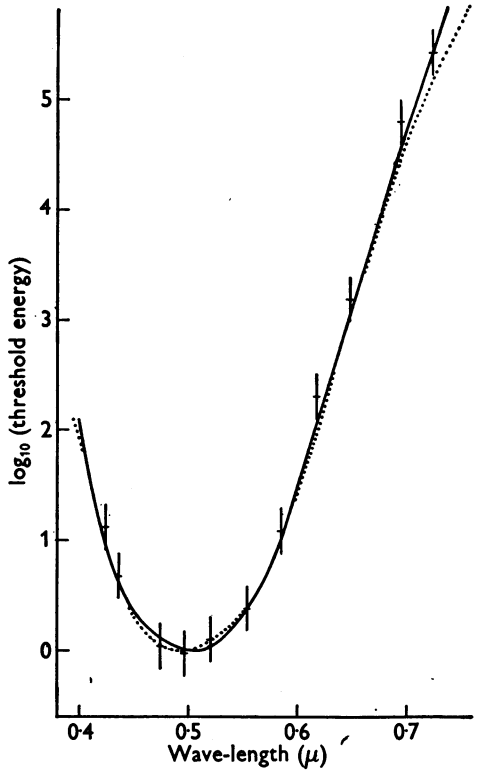

Fig. 7

Fig. 6. First approximation of the spectral threshold curves for two human subjects (arbitrary energy units). The black circles (●) refer to subject E. J. D. The other measurements refer to subject M. H. P.; series (+) and (○) were obtained on consecutive days, series (×) a year earlier. The scatter of the individual measurements for each filter is correctly represented but the positioning of each group of points on the log. energy scale is a first approximation. In energy units, the average threshold value for the most effective wave-length is here about 10^{-6} erg/sec × steradian × cm² (field).

Fig. 7. Comparison of the shape of our spectral threshold curve with the C.I.E. curve. The dotted line represents a mean curve based on the first approximation of Fig. 6. The crosses represent the second, and final, approximation. The vertical bars of these crosses give the estimated probable error of each determination. The full line represents the C.I.E. curve.

must determine in absolute units the spectral energy distribution of the light from the field (opal glass screen). This can be done on the basis of its intensity as determined in photometric units by the National Physical Laboratory.

In principle the luminance calibration could be made in the following way. First the light E'_λ emitted by the screen in watts per cm² of screen per unit solid angle (steradian) and per mμ would be determined using a physical measuring instrument. Then the standard C.I.E. photopic luminosity function V_λ (V_λ taken as unity at $\lambda = 0{\cdot}556\,\mu$) would be used and the luminance, F, of the

screen for white light in lm/cm² × steradian calculated (Walsh, 1926) from the equation

$$F = A\int_0^\infty E'_\lambda V_\lambda \mathrm{d}\lambda, \tag{4}$$

where A (the reciprocal of the so-called 'mechanical equivalent of light') is equal to 663 lumens/watt (Le Grand, 1948). The method used in practice may be considered to be equivalent to this theoretical method. It is therefore possible to calculate the absolute energy distribution of the light emitted by the opal screen on the basis of equation (4).

From the colour temperature of the light emitted by the screen we know

$$E_\lambda = \frac{E'_\lambda}{p}. \tag{5}$$

The arbitrary units in which E_λ was calculated were such that for $\lambda = 0{\cdot}59\,\mu$, $E_\lambda = 100$ per mμ. To find E'_λ we need only determine the proportionality factor p. From equations (4) and (5).

$$p = \frac{F}{A\int E_\lambda V_\lambda \mathrm{d}\lambda}. \tag{6}$$

For a colour temperature of 2400° K, we find by graphical integration $\int E_\lambda V_\lambda \mathrm{d}\lambda = 8545$. Thus for a flux $F = 1$ lm of this colour temperature, $p = 1{\cdot}76 \times 10^{-7}$ W.

It has been mentioned that under the conditions of the N.P.L. calibrations (opal glass screen 247·3 cm distant from the lamp, no wedges or filter in front of the lamp) the luminance of the screen was 0·0148 equivalent foot-candle, that is, $5{\cdot}06 \times 10^{-6}$ candela/cm². In a direction normal to its surface the screen thus emitted a flux $F' = 5{\cdot}06 \times 10^{-6}$ lm/steradian × cm². For this flux therefore we can define $p' = p \times 5{\cdot}06 \times 10^{-6}$. In the experiments on human threshold the distance between the source and the screen was 105·4 instead of 247·3 cm, so that the new flux F'' was greater than F' and the factor p' must be replaced by $p'' = (247{\cdot}3/105{\cdot}4)^2 \times p'$.

Consider the blue-green filter Ilford 604 which transmits from 0·49 to 0·55 μ (Fig. 5) and for which $\eta = \int E_\lambda T_\lambda \mathrm{d}\lambda = 98$. In a particular experiment the optical density of the wedges when set for threshold was 3·80. The total flux of energy at threshold was therefore

$$p'' \times \frac{\eta}{\text{antilog}_{10}\, 3{\cdot}80} = 7{\cdot}62 \times 10^{-7} \text{ erg/sec} \times \text{steradian} \times \text{cm}^2 \text{ (field)}. \tag{7}$$

On the basis of the C.I.E. scotopic luminosity function $S_\lambda = 1/H_\lambda$, this value can be corrected for the fact that the filter transmits a fairly wide spectral band, instead of transmitting monochromatic light of maximum effectiveness.

The correction amounts to about 7%, or 0·03 $\log_{10}$ unit, giving $7{\cdot}09 \times 10^{-7}$ erg/sec × steradian × cm² (field) for the corresponding value in light of $\lambda = 0{\cdot}51\,\mu$.

This energy value sets the spectral threshold curves on an absolute scale. Using the same filter 604, the mean threshold value for the two lowest series of measurements (+ and ○) of Fig. 6 was 0·11 $\log_{10}$ unit higher than in the above example. The lowest ordinate value of the curve representing these series must therefore be taken as equal to $\bar{7}{\cdot}96$ $\log_{10}$ units or $9{\cdot}15 \times 10^{-7}$ erg/sec × steradian × cm² (field). Thus the various measurements given in Fig. 6 lead to an average threshold value for the most effective wave-lengths of the order of 10^{-6} erg/sec × steradian × cm² (field).

The maximum compound error of the absolute energy scale in our measurements of the scotopic threshold curves appears to be of the order of $\pm 0{\cdot}10$ $\log_{10}$ unit. It is possible, however, that some of the measurements, such as those made with filter Ilford 604, are more accurate than this.

The above values for the flux of energy refer to a direction near the normal to the surface of the luminous field. The opal screen, however, radiates energy in all directions. On the assumption that the screen is a perfect diffuser obeying Lambert's law, the total radiation emitted on the side of the subject would be equal to the above values multiplied by the factor π. The values given in Fig. 1 of our communication on the visual threshold of *Xenopus laevis* (Denton & Pirenne, 1951) are total radiation values calculated in this way. Whilst the assumption that the screen is a perfect diffuser is probably incorrect, the exact values for the flux (per steradian) normal to the surface can in any case be obtained by dividing by π the energy values of the above communication.

Absolute threshold measured with white light

The same apparatus has been used (Pirenne, 1943, unpublished report to the Military Personnel Research Committe) to study individual differences of visual acuity at low luminance levels in a group of twenty-three young human subjects. In this investigation the absolute threshold of a few subjects was measured under conditions similar to the above (continuously exposed field subtending 47° at the eye, binocular vision), but using white instead of coloured light. These direct measurements, as well as acuity measurements made at a luminance equal to twice the absolute threshold, lead to a mean log. value of $\bar{7}{\cdot}93$ $\log_{10}$ unit, or $0{\cdot}85 \times 10^{-6}$ cd/m². The lowest individual $\log_{10}$ threshold value in the group is $\bar{7}{\cdot}6$ ($0{\cdot}4 \times 10^{-6}$ cd/m²) and the highest $\bar{6}{\cdot}7$ (5×10^{-6} cd/m²). The distribution of the individual log. values is skew, 14 out of 23 subjects having a value below the mean.

These results agree with those obtained by other workers. The absolute threshold for large fields and long exposures is known to be of the order of

10^{-6} cd/m^2 (Weinstein & Arnulf, 1946; Le Grand, 1948). In one subject, Weinstein & Arnulf (1946), using light of practically the same colour temperature (2390° K) as in the present investigation (2400° K), found a threshold value as low as $0{\cdot}28 \times 10^{-6}$ cd/m^2. This was obtained uniocularly using a continuously exposed field 8° in diameter. (In the case of one other subject, Weinstein & Arnulf (1946) report a threshold of $0{\cdot}13 \times 10^{-6}$ cd/m^2. In a private communication, however, Prof. Arnulf says that this exceptional result is not as certain as the preceding one, which refers to a very reliable subject.)

In our experiments we found that the threshold value obtained using both eyes was very near the value obtained for the more sensitive of the two eyes used separately. Under conditions giving frequency curves having an uncertainty range of the order of 1 $\log_{10}$ unit, the binocular threshold is only about 0·1 $\log_{10}$ unit below the uniocular, and this difference can be explained by the greater probability of seeing, with at least one of the two eyes, when both eyes are used (Pirenne, 1943). Since in the present experiments the frequency-of-seeing curves are markedly steeper the very small difference found between binocular and uniocular vision is understandable. Crawford (1940), using a test field 0·67° in diameter exposed in 1 sec flashes, found that the binocular absolute threshold was only 0·03 $\log_{10}$ unit lower than the uniocular.

Light of $0{\cdot}51\,\mu$ *equivalent to white light.* It is easy to calculate the energy flux $Q\,(0{\cdot}51\,\mu)$ of the light of $\lambda = 0{\cdot}51\,\mu$ having the same scotopic effectiveness as a given flux F of white light expressed in lumens if the spectral distribution of energy E_λ in the white light is known. It is

$$Q\,(0{\cdot}51\,\mu) = \frac{F}{A} \times \frac{\int E_\lambda S_\lambda \mathrm{d}\lambda}{\int E_\lambda V_\lambda \mathrm{d}\lambda} = \frac{F}{A} \times R, \tag{8}$$

where R may be called the scotopic/photopic ratio of the light of spectral energy distribution E_λ.

Special measurements were made with one subject at a single sitting in order to compare directly the threshold for white with that for the blue-green light transmitted by filter 604. Experimental conditions were kept the same except for the presence or absence of the colour filter. Taking into account the spectral transmission of the 'neutral' wedges (Fig. 2), the results were in excellent agreement with those predicted by equation (8). (The calculations also show that if we had assumed that the wedges were perfectly neutral for white light, we would have obtained values about 0·1 $\log_{10}$ unit too high.)

The mean threshold for white in our group of subjects is $0{\cdot}85 \times 10^{-6}$ cd/m^2. On the basis of equation (8) this is equivalent, in light of $0{\cdot}51\,\mu$, to a flux of energy

$$B = 5{\cdot}9 \times 10^{-7} \text{ erg/sec} \times \text{steradian} \times \text{cm}^2 \text{ (field)}. \tag{9}$$

This value, which is of the same order as that obtained above for two subjects using a blue-green filter, will be taken here as an average value of the threshold of normal young subjects. Although derived from binocular observations, it may be considered as referring to the more sensitive of the two eyes. Since the lack of neutrality of the wedges for white light has not been taken into account (the error involved is smaller here than in the preceding example), the value may be slightly too high. This may not be a disadvantage in some theoretical discussions. It will also be remembered that the threshold of our most sensitive subject was about half the mean value for the group.

The minimum retinal illumination

The retinal illumination D is (Le Grand, 1948)

$$D = 0{\cdot}36\tau s B, \tag{10}$$

where τ is the transmission factor of the eye from the cornea to the retina for the light used, s the area of the pupil in cm^2 and B the luminance of the extended field of view. Here the luminance is expressed as above in erg/sec × steradian × cm^2 (field). The retinal illumination D is then expressed in erg/sec × cm^2 (retina).

The transmission factor of the refractive media of the eye is not known with a high degree of certainty, particularly in the case of extended fields. It is possible that the light losses are due to scattering rather than to true absorption in the eye media, in which case the effective loss would be smaller in the case of a large than a small field (Le Grand, 1948). The available measurements (Ludvigh & McCarthy, 1938) give $\tau = 0{\cdot}50$ for $\lambda = 0{\cdot}51\,\mu$. The light losses due to reflexions at the air-cornea interface amount to about 2% (Le Grand, 1946).

We will take $\tau = 1$, which must lead to an upper value of D. Thus it will be assumed that all the light striking the cornea reaches the retina without loss. This should ensure that there is no under-estimation of the retinal illuminations calculated here. If it appears desirable, it will be easy to apply a correction based on a particular estimate of τ, taking into account the small loss due to corneal reflexion, which is here neglected.

At the absolute threshold, the average pupil has an area s of about 0·5 cm^2 (Le Grand, 1948). Thus, taking the value of B given by equation (9), we find

$$D = 1{\cdot}06 \times 10^{-7} \text{ erg/sec} \times \text{cm}^2 \text{ (retina)}. \tag{11}$$

This is equivalent to 9×10^{-11} erg/sec striking the retina per square degree of the external field. For $\lambda = 0{\cdot}51\,\mu$, the energy of a light quantum is $3{\cdot}89 \times 10^{-12}$ erg. The illumination D therefore corresponds to 27,300 quanta/sec × cm^2 of the retina; that is to 23 quanta reaching the retina per second from each square degree of the field. (If losses in the eye media are not to be neglected, these values represent the corresponding amounts of light at the cornea of the eye.)

It might be emphasized that when light quanta are used in this way to

express amounts of radiating energy reaching the eye, or to express retinal illuminations, it should not be taken as suggesting that the light flux does really behave like a stream of particles, each of which would be a quantum—a view which would of course lead to completely mistaken conclusions regarding diffraction and interference phenomena. In the present case it is only when light is absorbed by retinal receptors that quantum considerations become applicable. Then it can be said, for instance, that a quantum has been absorbed in a certain rod. But as long as no absorption has taken place the quanta cannot be localized and the only information we can have is the probability distribution of the radiating energy reaching the retina. Such a phrase as 'a mean illumination of y quanta ($\lambda = 0{\cdot}51\,\mu$) per rod per second' merely means that the mean flux of radiating energy reaching the rod is equal to $y \times 3{\cdot}89 \times 10^{-12}$ erg/sec. The quantum is used simply as a convenient unit of energy; if the probability of light absorption by a rod is x, the mean number of quanta absorbed per second is xy.

Quanta absorbed in the rods. According to Østerberg's measurements (which refer to one particular human retina), the periphery of the retina at eccentricities between 20 and 40° on the horizontal meridian contains an average of about 134,000 rods and 5250 cones per mm² (Østerberg, 1935). Schultze's drawings of unfixed retinal preparations show that in this region each cone occupies an area equivalent to that which would be occupied by about seven rods (Schultze, 1866; drawing reproduced in Pirenne, 1948). Further, if the rods are arranged like closely packed cylinders, their cross-sections have an area equal to 0·907 of that of the full cross-section. Thus the area of the cross-sections of the rods is equivalent to

$$0{\cdot}907 \times 134{,}000/[134{,}000 + (7 \times 5250)] = 0{\cdot}7 \qquad (12)$$

of the retinal area under consideration. This value is too high if the rods are not closely packed. (Assuming close packing, the diameter of a rod would be $2{\cdot}6\,\mu$.) We have little information on the refraction and scattering to which the light incident on the layer of rods and cones may be submitted. Here we will take it that a proportion 0·7 of the light strikes the rods while the rest, 0·3, is lost as far as rod vision is concerned. If f is the proportion of the light incident on the *retina* which is absorbed by the rods, the proportion of the light striking the *rods* and absorbed by them will therefore be $x = f/0{\cdot}7$.

Assuming an absorption probability $f = 0{\cdot}1$, or $x = 0{\cdot}143$, for $\lambda = 0{\cdot}51\,\mu$, and assuming that there are no losses in the eye media ($\tau = 1$), the mean amount of light absorbed per second by the rods in a peripheral retinal region corresponding to 1 square degree of field would be $23 \times 1 \times 0{\cdot}1 = 2{\cdot}3$ quanta at threshold. Such a region is $8{\cdot}47 \times 10^{-4}$ cm² in area and contains about 11,350 rods. Thus for $\tau f = 0{\cdot}1$, the mean absorption would be about 1 quantum/sec/5000 rods.

The probability f is not accurately known and may vary from one individual to another. A direct estimate of f was obtained in one case by extracting the visual purple from a human retina and measuring its optical density *in vitro* (König, 1894); it gave $f=0{\cdot}04$. We shall see presently that such estimates may be too low because the dichroism of the rods may favour the absorption of the light reaching them in their natural position in the eye.

It might theoretically be possible to obtain an indirect estimate of x, and therefore of f, by comparing the shape of the sensitivity curve, calculated on a quantum basis at the retina, with the shape of the absorption spectrum of rhodopsin measured *in vitro*. Hecht *et al.* (1942) made such calculations, as a result of which they took 0·20 as an upper limit of f in order 'to be quite safe'. This comparison cannot any longer be considered reliable, however, because the human sensitivity curve used by Hecht *et al.* was broader than the new C.I.E. curve and probably inaccurate (Crawford, 1949). Stiles (1948) made a new comparison of the relevant curves. For $\lambda>0{\cdot}43\,\mu$, it shows rather small differences between the human scotopic sensitivity curve and the absorption curve of frog rhodopsin for infinite dilution. These differences are not easy to interpret. There is no clear indication of broadening due to the finite concentration of rhodopsin in the rods. But in any case a considerable amount of uncertainty remains in the present connexion, particularly on account of Schmidt's observations. Schmidt (1938) has shown that the red-coloured rods of the frog are naturally dichroic, light absorption being maximum, for an absorbing layer of a given thickness, for light falling along the axis of the rod. It is therefore most likely that in the rods the rhodopsin molecules are not oriented at random as in solution but are arranged in preferred positions. Such an arrangement might possibly alter the shape of the absorption curve *in situ* compared to that *in vitro*. Even if this complication does not arise, Schmidt's important findings prove that absorption *in situ* in man may well be higher than the absorption calculated from measurements made on solutions containing the whole of the rhodopsin present in the retina.

Bearing this possibility in mind, and remembering König's estimate of 0·04, it seems reasonable at the present time to take $f=0{\cdot}1$ as a basis for discussion. This is an arbitrary choice, but it should be easy to modify the conclusions reached on this basis if definite information about f (and τ) becomes available and makes the alteration necessary. The present choice gives $\tau f=1\times0{\cdot}1=0{\cdot}1$, whereas Hecht *et al.* took $\tau f=0{\cdot}96\times0{\cdot}50\times0{\cdot}20=0{\cdot}096$, a very similar value. An independent argument given at the end of the discussion of 'The possibility of spontaneous excitation in the retina' leads to a tentative value of about 0·07 for τf, in the case of a 10′ test field.

The threshold measured in terms of the luminance of the external field is different in individuals; it can also vary from day to day in a given individual. It is not known whether such variations are related to changes in τf, and more

particularly in f, that is to changes in the concentration of rhodopsin in the rods. The values of τ and f in individual living eyes are less well known than their mean values.

DISCUSSION

Assuming that $\tau f = 0{\cdot}1$, it has been seen that the threshold corresponds to an average of 1 quantum absorbed every second per 5000 rods. The chance of one rod absorbing two or more quanta within the retinal action time, about 0·1 sec, is therefore small. Threshold stimulation must occur mostly through the summated effects of the absorption of single quanta in individual rods which may be at some distance from one another.

Since the retina is not homogeneous in its properties it is probable that, among the functional receptor units contained in the area covered by the image of the whole field, only those having the highest degree of spatial and temporal summation are responding at threshold. Each of the retinal units referred to here probably consists of a number of receptors linked to an optic nerve fibre. Their mode of action has been discussed elsewhere (Pirenne & Denton, 1952). Since the mean retinal illumination is very low, the number of quanta absorbed by these units must fluctuate considerably. It seems reasonable to assume that the test field is seen when at least one, or a few, such units have by chance absorbed a minimum number of quanta within their action time. This minimum number must be greater than one per unit and it is probably smaller than 10 (Pirenne, 1951). According to the simple interpretation of the spectral sensitivity curve (Stiles, 1948) this number of absorbed quanta would be independent of wave-length.

Functional stability of the retina

Various considerations (Denton & Pirenne, 1952) suggest that under favourable conditions the retina is not only extremely sensitive, but also can function with a high degree of stability. It is possible to draw some general conclusions on this stability from the frequency-of-seeing curves described under Results. The curves of Fig. 3 show that, according to the subject, the range of uncertainty of seeing covered 0·3 or 0·4 $\log_{10}$ unit; that is, it extended in relative units from intensity 1 to intensity 2 or 2·5. In other words, in a series of all the random trials made at one single sitting as described under Methods and Results, one of the subjects, for instance, never reported 'seen' at intensity 1 or under, and always reported 'seen' at intensities 2 and above. It can be concluded from this that the *average* biological sensitivity during each one of the trials made at one sitting did not vary beyond these limits. If in one or more trials the average sensitivity of this subject had corresponded, for instance, to intensity 2·5, the frequency of seeing at this intensity level would of course have been less than 100%, whereas it was 100%.

The use of a large test field, long exposure and binocular vision is likely to reduce the effect of quantum fluctuations and other random variations on the range of uncertainty of seeing. Each one of the present 5 sec trials can theoretically be considered as consisting of a number of attempts by the subject to see the test field, each attempt corresponding probably to one 'look', that is, to a fixation pause in the continual movements of the eyes. Each of these 'looks' in turn involves, in each retina, all those functional units which correspond to the image of the test field. Thus, each 5 sec trial may be considered as consisting of a large number of more or less independent attempts at the stimulation of one or a few out of a large number of retinal units. On general statistical grounds, the accuracy of the threshold determination should accordingly be increased, rather as the accuracy of the determination of a physical quantity is in general increased when repeated measurements of this quantity are made. Exact calculations can hardly be carried out because it is not known to what extent these individual stimulations can be considered as statistically independent. Information is also lacking on the characteristics of the functional units of the periphery of the retina which are likely to be active under the present conditions.

In the present experiments, therefore, the influence of the purely physical quantum fluctuations on the frequency-of-seeing curve must be smaller than in experiments using a small test field and a short flash, in which case the observed range of uncertainty is of the order of 1 $\log_{10}$ unit. These fluctuations are probably not negligible, however. Since in all cases the observed curve must be determined by a combination of variations of biological sensitivity, of quantum fluctuations, and of other possible sources of variation, the two latter causes will tend to increase the range of uncertainty of seeing which would be caused by biological variations alone. The above ranges for the variability of the biological sensitivity during 5 sec trials, 0·3–0·4 $\log_{10}$ unit, must therefore be considered as upper limits.

Thus, in the present experiments the *average* biological sensitivity of the visual system taken as a whole—eye, brain and motor mechanisms—cannot have varied from one 5 sec trial to another by more than $\pm 0{\cdot}2$ $\log_{10}$ unit, and may have varied by less than this value. Larger biological variations may possibly have occurred during the course of each 5 sec trial, but this does not affect the above conclusion.

It may perhaps be emphasized that this reasoning refers exclusively to the average sensitivity during the individual 5 sec trials and does not give any information about the sensitivity of the subject in the intervals of rest between trials. It will be remembered that the exposure was not continuous and that the subject was free to choose his own time for each trial. Assuming that the subject goes through periods of heightened and lowered sensitivity during an experiment, the present method may help to eliminate the influence of the

periods of lower sensitivity, and thus lead to more constant results than when the stimulus is presented to the subject at intervals chosen by the experimenter. It must also be borne in mind that under unfavourable conditions (fatigue, etc.) the observed frequency-of-seeing curves have a larger range of uncertainty and the visual system then obviously functions in a less stable manner than in the experiments just discussed.

The possibility of spontaneous excitation in the retina

It is generally accepted that light acts on the retinal receptors by bleaching some of the sensitive substances they contain. For $\lambda > 0{\cdot}43\,\mu$, the bleaching spectrum of frog rhodopsin agrees reasonably well with its absorption spectrum. As Stiles (1948) has shown in the above-mentioned discussion, these spectra also agree fairly well with Crawford's redetermination of the human scotopic visibility curve after suitable corrections have been applied to the latter. This gives further confirmation to the view that the photosensitive substance in the human rods is very similar to frog rhodopsin.

Now experiments *in vitro* show that the bleaching of frog or cattle rhodopsin also occurs in the absence of light, the rate of this 'dark', thermal reaction increasing rapidly with temperature. Such a spontaneous bleaching of rhodopsin may therefore occur in the living retina. It might possibly be related to the spontaneous activity often observed in electrophysiological experiments on animal retinae. This raises an important problem, for the spontaneous reaction might be expected to interfere strongly with the reception of light stimuli. But, on the other hand, the values of the retinal illumination at threshold are so low that they seem hardly compatible with any marked degree of spontaneous activity. The problem can be approached quantitatively on the basis of the latter observation, using 'signal/noise' considerations of a kind familiar to physicists.

Assume that a molecule changed by the dark reaction is capable of causing in the rod cell to which it belongs the same reactions as a molecule changed by the absorption of a light quantum. The dark reaction ('noise') will then determine a certain level of spontaneous nervous excitation in the living retina. If this random 'noise' exceeds a certain level, its continual fluctuations in time will make it impossible to detect a light stimulus ('signal') below a certain intensity. On this basis, regarding the spontaneous activation of rhodopsin molecules as the only source of noise, we will try and calculate the maximum noise level compatible with the intensity of the smallest detectable stimuli; that is, with the absolute threshold intensity as determined under various conditions.

The following symbols and definitions will be used:

N Number of chromophoric groups contained in the rods covered by the retinal image of a peripheral field subtending 1 square degree at the eye.

K Mean number of chromophoric groups spontaneously activated per second in a peripheral retinal area corresponding to 1 square degree.

$k = K/N$.

a Retinal area inside which complete physiological summation takes place, in square degrees.

t Retinal action time in seconds; that is, the time during which complete physiological summation of the stimulus takes place.

τ Light transmission factor of the eye media for $\lambda = 0{\cdot}51\,\mu$. The factor τ is supposed also to take into account the light losses due to reflexion at the air-cornea interface. In this paper we generally take $\tau = 1$.

f Proportion of the light ($\lambda = 0{\cdot}51\,\mu$) incident on the retina which is absorbed by the rods of the corresponding retinal region. We generally take $f = 0{\cdot}1$.

x Proportion of the light ($\lambda = 0{\cdot}51\,\mu$) incident on a rod which is absorbed by this rod; x may be taken as equal to $f/0{\cdot}7$ (see Retinal illumination).

ϕ Quantity of light ($\lambda = 0{\cdot}51\,\mu$), expressed as a number of quanta, striking the cornea per second per square degree of external field at threshold.

α Extinction coefficient per chromophoric group expressed in cm^2 and defined by the equation

$$\log_e \frac{I}{I_t} = \alpha N' \frac{l}{v}, \tag{13}$$

where I is the incident light intensity, I_t the transmitted light intensity, N' the number of chromophoric groups present in the absorbing layer, v the volume of the absorbing layer and l its thickness. This is valid for rhodopsin in solution but may require modification in the rods themselves on account of their dichroism.

We take as the 'signal' the number of quanta absorbed at threshold by the rods in the area a during the time t; this is $\tau atf\phi$. Within the same time and area, the mean number of chromophoric groups spontaneously activated is atK. The activations which constitute the 'noise' must be expected to occur at random; the standard deviation from the mean number therefore is $\sqrt{(atK)}$. If we assume that in order to be seen the 'signal' must be at least 3 times this standard deviation, we have

$$\tau atf\phi \geqslant 3\sqrt{(atK)}. \tag{14}$$

Hence

$$K \leqslant \tfrac{1}{9}\,\tau^2 atf^2\phi^2. \tag{15}$$

This equation applies to the case of a light flash of duration equal to the action time t and falling exactly upon a retinal area a in which complete summation occurs. According to the measurements of Graham & Margaria (1935), a flash 0·1 sec in duration and 1 square degree in area probably represents an approximation to these conditions. Its threshold energy content

is of the order of 200 quanta, which corresponds to $\phi = 2000$. If we take $f = 0{\cdot}1$ and $\tau = 1$, we have

$$K \leqslant \tfrac{1}{9} \times 0{\cdot}1 \times (0{\cdot}1)^2 \times 2000^2 = 444. \tag{16}$$

Thus, during the action time, the signal would be 20 quanta and the noise would be 44, or less than 44, chromophoric groups excited. (The total number of molecules involved is so large that each of the groups spontaneously excited must belong to a different molecule.)

On account of insufficient knowledge concerning the functional organization of the retina, and consequently of the mechanisms of spatial and temporal summation, it is not easy to decide if there are experimental arrangements which give a better approximation to t and a than the preceding example. In the periphery, fairly complete spatial summation is generally found to occur up to a field diameter of 1 or even 2°, after which there is a certain range of incomplete summation. For a field 1 or 2° in diameter, temporal summation is fairly complete only for durations up to about 0·01 sec and incomplete summation occurs in a certain range of longer durations (Graham & Margaria, 1935). We made a direct measurement of the threshold in one subject using a field $2\sqrt{2}°$ in diameter and a flash lasting 0·1 sec. The 50% threshold value was 280 quanta. Applying equation (15), this gives $K \leqslant 139$. This is less than the above value $K \leqslant 444$, which will be retained as a safer basis for discussion. In the case of a field 47° in diameter exposed for 5 sec, we have $\phi = 23$. If, for the sake of argument, we treat the whole field as a single unit of area $a = 1740$ and having an action time $t = 5$ equal to the duration of the whole exposure, we find $K \leqslant 5100$, which is only about one power of 10 higher than 444.

According to Dartnall, Goodeve & Lythgoe (1938), the probable value of α is 9×10^{-17} cm^2 for $\lambda = 0{\cdot}506\,\mu$. On the basis of equation (13) this links N with x and f, since $I_t = I(1-x)$. The retinal area corresponding to 1 square degree is $8{\cdot}47 \times 10^{-4}$ cm^2 and the total cross-section of the 11,350 rods it contains is $5{\cdot}93 \times 10^{-4}$ cm^2. This cross-section here corresponds to the ratio v/l of equation (13). Thus

$$N = -1{\cdot}52 \times 10^{13} \log_{10}(1 - f/0{\cdot}7). \tag{17}$$

For $f = 0{\cdot}1$, $N = 1{\cdot}02 \times 10^{12}$. (On the same basis the number of chromophoric groups per human rod is $8{\cdot}98 \times 10^7$.) Thus the fraction of chromophoric groups spontaneously activated per second is

$$k = K/N \leqslant 444/(1{\cdot}02 \times 10^{12}) = 4{\cdot}4 \times 10^{-10}. \tag{18}$$

Equations (15) and (17) show that if f is taken as variable, the value of k is proportional to $-f^2/\log_{10}(1-f/0{\cdot}7)$. The function $y = -x^2/\log_{10}(1-x)$ is maximal for $x = 0{\cdot}715$, when $y = 0{\cdot}94$. Now for $f = 0{\cdot}1$ or $x = 0{\cdot}143$, $y = 0{\cdot}30$, so that for $x = 0{\cdot}715$ or $f = 0{\cdot}5$ we must have

$$k \leqslant 4{\cdot}4 \times 10^{-10} \times (0{\cdot}94/0{\cdot}30) = 1{\cdot}38 \times 10^{-9}. \tag{19}$$

Thus, simple signal/noise considerations suggest that k is not greater than $1{\cdot}4 \times 10^{-9}$. There is no evidence to suggest that f is as high as 0·5 in the human eye. Again, it is likely that τ is markedly smaller than unity. The above k value therefore should be an upper value. It corresponds to only 0·0005 %/hr for the fraction of the rhodopsin present in the rods which undergoes spontaneous activation.

If dichroism exists in human as in frog rods, the true value of N is smaller than that calculated above and the value of k becomes higher. But this should not markedly decrease the wide gap which exists between values of k calculated *in situ* and observed *in vitro*, the latter values being at least 1000 times higher than the former.

The experiments of Lythgoe & Quilliam (1938) on the thermal decomposition of frog rhodopsin *in vitro* indicate a rate of about 5 %/hr at pH = 7 at 37° C. Again, St George (1952) gives results which would correspond to about 1 %/hr for cattle rhodopsin at the same temperature.

There is no necessary contradiction between these results and the above calculations. The apparent heat of activation determines the variation of k with temperature, but the *absolute* rate of decomposition depends on various factors which do not affect this heat of activation. Lythgoe & Quilliam (1938) found the apparent heat of activation to be independent of the pH, whereas the pH affects strongly the absolute rate of bleaching. In the intact rod, the rhodopsin molecules are probably submitted to particular constraints which do not exist in the case of a solution. Factors such as these must affect the entropy term, independent of temperature, which enters besides the apparent heat of activation in the equation giving the absolute reaction rate (Stearn, 1949). *In vitro* the process of activation may be accelerated by the larger increase of entropy which follows from the reaction. Thus there is no theoretical objection to the absolute reaction rate *in situ* being much lower than *in vitro*.

Making some further assumptions on the functioning of the retina, it is possible to show that in the case of a small field the noise probably plays only a minor part at threshold, being too weak to limit the absolute sensitivity of the retina. If the rods contained in a retinal area (1 or 2° in diameter) in which a high degree of spatial summation occurs were all connected to one single optic nerve fibre, we should expect spontaneous excitation from the whole area to be summated towards this final common path independently of whether the light stimulus itself covers the whole retinal area or only a part of it. Even on purely anatomical grounds, however, it is unlikely that the human retina is organized in such a simple manner. In a discussion of the accuracy and sensitivity of the eye, Pirenne & Denton (1952) have suggested that while the rods do form large functional units of the kind just described, the same rods are also connected in a different way forming smaller functional units, each of which possesses its own optic nerve fibre. At sufficiently high intensities the

small units would absorb enough quanta to respond, but at the lowest intensities they would not, only the largest units summating enough light to remain active. If the retina works in this way, it seems probable that the smaller units summate only the noise occurring within their own receptive field and are unaffected by noise occurring in neighbouring units. Making the simplifying assumption that when a small test field is used its image covers approximately one of the smaller units, only the noise occurring in the retinal area covered by the image of the field has to be taken into consideration, as a first approximation.

Consider threshold measurements made with a field 10′ in diameter, that is 0·022 square degree in area, and with a flash of 0·001 sec duration. The threshold value corresponds to an average of 100 quanta at the cornea. For $\tau=1$ and $f=0{\cdot}1$, this means a 'signal' of 10 quanta absorbed. This signal should be compared with the noise value, not for 0·001 sec, but for the action time, about 0·1 sec. According to the estimate of equation (16), this is equal at the most to forty-four spontaneous decompositions per square degree. According to the assumption discussed in the preceding paragraph, the upper value of the noise would then be equal to $44\times0{\cdot}022=0{\cdot}97$. The mean noise per flash would thus be at the most 1 spontaneous activation, whereas the mean value of the signal would be 10 quanta.

The effect of such a weak random background should be similar to that of biological variations of sensitivity rarely exceeding the equivalent of 1 or 2 quanta. The influence of such variations on the frequency-of-seeing curve has been discussed by Hecht *et al.* (1942) and by Pirenne (1951). It would hardly affect the general analysis of the results on the basis of the Poisson probability equation given in the original paper of Hecht *et al.* (1942). This analysis led to values ranging from 5 to 8 for the number of quanta which must be absorbed at threshold. The product τf should therefore be about 0·07 instead of 0·10 as assumed above. But according to equation (15) the upper value of K would be halved if $\tau f=0{\cdot}07$ instead of 0·10. Thus the upper value of the noise would be only 0·5 against a mean signal strength of about 7 quanta. In the present connexion it may be pointed out that we do not think that the theory according to which the minimum quantity of light necessary for vision would be 2 quanta absorbed by the retina (van der Velden, 1944; Bouman & van der Velden, 1947) is sufficiently proven by the evidence given in support of it (Pirenne & Denton, 1951). But in any case it seems that this theory could only lead to a lower value of the noise as calculated here.

It is conceivable, but unlikely, that, contrary to the hypothesis made at the beginning of this discussion, thermal activation and light activation do not act in the same way on the molecules, thermal activation being unable to cause nervous excitation. The rate of spontaneous activation could then be as high *in situ* as *in vitro* without producing any effective noise interfering with

the reception of the light signal. If, on the other hand, rods could become spontaneously excited through some process which does not involve rhodopsin, this again could produce noise in the retina.

In general, if spontaneous excitation is *of a different kind from the action of light on the visual system*, such excitation may be ineffective as noise in the present sense. It seems clear that the total amount of *effective* noise of all origins cannot exceed a level corresponding to that calculated above in terms of activated molecules. (Perhaps it is possible that the spontaneous excitation observed in some electrophysiological preparations is not effective noise in the present sense.)

In conclusion, the effective noise in the living retina must be of much lower intensity than the value derived directly from the study of rhodopsin solutions. If it were as high as this value, the retina should be incapable of detecting the weak threshold stimuli which in fact it can detect. It should also be incapable of detecting stimuli of a few times threshold strength, whereas the latter can be seen most distinctly (see Results) and look much brighter than the phosphenes observed under normal conditions. The effective noise may possibly be much lower than the value given in equation (19) and always play a negligible role even at the absolute threshold. There is no evidence to prove that this is not so. Finally, even if spontaneous retinal excitation plays a part at the absolute threshold, it must soon become negligible at supra-liminal intensity levels.

Photochemical bleaching of rhodopsin in situ

According to the values taken as a basis for discussion in this paper (1 quantum absorbed among 5000 rods/sec; 7×10^7 chromophoric groups contained in one rod), and assuming that the quantum efficiency of rhodopsin bleaching is unity, it is seen that at threshold only 1 in every $3{\cdot}5 \times 10^{11}$ chromophoric groups is bleached by light every second. Accordingly, at an intensity of 1 cd/m^2, that is at a level at which cones are functioning actively, 1 million times above the rod absolute threshold, the fraction of retinal rhodopsin bleached will be only 1 %/hr. Thus the purely photochemical aspect of light adaptation should remain almost negligible even at such an intensity level. This confirms the view (Baumgardt, 1950) that certain theories of vision based on photochemical considerations will have to be reconsidered on the basis of the absolute sensitivity of the retina.

Note added in proof. Crescitelli & Dartnall (1953) have recently studied the rhodopsin extracted from a dark-adapted human retina. They find good agreement between the absorption spectrum of their preparation of human rhodopsin and the human scotopic function of Crawford (1949), suitably corrected. Thus it is likely that the relatively minor but rather puzzling

discrepancies, referred to in the present paper in connexion with Stiles's discussion (1948), can largely be accounted for by differences between the spectra of frog and human rhodopsin. The optical density of the extract obtained by Crescitelli & Dartnall would correspond to a value $f=0{\cdot}035$, which is very close to Konig's (1894) estimate, $f=0{\cdot}04$, taken into account in the present paper.

REFERENCE

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SUMMARY

1. The absolute threshold of the human eye to a test field subtending about 45° at the eye and exposed for about 5 sec at each trial was measured. The subject used ordinary binocular vision with natural pupils, without fixation. Measurements were made with narrow bands of the spectrum isolated by colour filters and also with the white light emitted by the tungsten filament lamp used as a source.

2. In the case of spectral bands, the threshold flux of radiating energy was calculated on the basis of the candle-power and colour temperature of the light source. The shape of the spectral sensitivity curves thus obtained for two subjects agrees with the recently adopted international scotopic curve. It was verified by direct experiments that, on the basis of this curve, the absolute threshold value for blue-green light is equivalent to the value for white light.

3. The average absolute threshold for white light (colour $T=2400°$ K) in a group of twenty-three young subjects was at $0{\cdot}85\times10^{-6}$ cd/m^2 (field). This is equivalent in light of $0{\cdot}51\,\mu$ to a flux of $5{\cdot}9\times10^{-7}$ erg/sec per steradian per cm^2 of the test field.

4. Neglecting light losses from cornea to retina, the above value for light of $0{\cdot}51\,\mu$ corresponds to a mean retinal illumination of 27,300 quanta per cm^2 of retina per second. If the effective absorption by the rods is 10% of the light striking the cornea, this corresponds to a mean value of 1 quantum of light absorbed every second per 5000 rods. In round figures, the total amount of light entering the eye during one 5 sec exposure is of the order of 200,000 quanta, whereas the retinal image of the field covers about 20 million rods.

5. The frequency-of-seeing curve for large fields and long exposures is much steeper than that obtained for small fields and brief flashes. The shape of the curve shows that the average biological sensitivity of the visual system cannot vary from one 5 sec trial to another by more than $\pm0{\cdot}2$ $\log_{10}$ unit.

6. The possibility of spontaneous excitation in the retina ('noise') is discussed on the basis of 'signal/noise' considerations, the light stimulus being the 'signal'. It is estimated that, if spontaneous decomposition of rhodopsin similar to activation by light occurs in the living rods, it must do so at a rate less than 0·001%/hr, that is at least 1000 times slower than *in vitro*. The

conditions of the rhodopsin molecule may be very different in the rods and in solution. It is possible that the effective 'noise' in the retina is of negligible importance even at the absolute threshold.

7. From the value of the absolute threshold for a large field, it is estimated that the fraction of retinal rhodopsin bleached in the rods must be of the order of only 1 %/hr at a light intensity of 1 cd/m^2 (field).

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