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INCREMENT THRESHOLDS AT LOW INTENSITIES CONSIDERED AS SIGNAL/NOISE DISCRIMINATIONS

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It was shown by Hecht, Shlaer & Pirenne (1942) and Van der Velden (1944, 1946) that the quantal nature of light is largely responsible for the variability of response of human subjects to near-threshold visual stimuli. At about the same time Rose (1942, 1948) and de Vries (1943) suggested that the inescapable variability in the number of quanta absorbed from a constant light limits the accuracy with which its intensity can be judged, and that the differential threshold is set at as low a level as is compatible with this limit. If this suggestion is correct, one's concept of the nature of a psycho-physical threshold needs to be altered considerably; instead of recalling the all-or-nothing behaviour of a nerve fibre, one should consider the 'threshold' of sensitivity of a galvanometer which is constantly perturbed by noise, or some other example of a limit which is set in accordance with statistical criteria. It has been shown that such a view of the nature of threshold is entirely compatible with the data for the absolute sensitivity of the eye if it is assumed that there is a certain low level of intrinsic retinal noise, even in complete darkness (Barlow, 1956). In the present paper an attempt is made to determine the value of this retinal noise, and to test whether the idea that thresholds are efficient statistical judgements of constant fallibility, can be applied to the differential threshold of the human eye at low intensities.

Historical background

The history of the measurement of the difference threshold, and of the generalizations based on these measurements, can be found in von Helmholtz (1924), Hecht (1924), and Le Grand (1950). For one interested in understanding the physiological mechanisms underlying such thresholds the sequence of events is discouraging. Two centuries ago Bouguer (1760) made observations of his ability to detect the shadow cast by one candle when the screen upon which the shadow fell was simultaneously illuminated by another candle. These measurements were of sufficient accuracy to show that the ratio $\Delta I/I$ (least detectable increment of intensity/absolute intensity) stayed more nearly constant than did the absolute values of ΔI. During the next century these observations were confirmed and extended in range, and in 1860 Fechner published his *Elemente der Psychophysik* in which the constancy of $\Delta I/I$ was exalted to the status of a general law. This general law was promptly shown to break down both at low and high intensities (Aubert, 1865), and also in the intermediate range (von Helmholtz, 1924). The inaccuracy of the law was confirmed by the extensive and accurate measurements made by König & Brodhun in 1888–9 (König, 1903). In summary, they showed that the fraction $\Delta I/I$ decreases from a value of about 0·6 to about 0·02 as the absolute intensity is increased through 3 log. units (for red light) or 5 log. units (for blue light) from a starting level of intensity about 10 × the absolute threshold; the fraction remains roughly constant at this low level for about 2 more log. units, and then increases slightly as the intensity is increased further. Later workers (e.g. Blanchard, 1918; Stiles & Crawford, 1933, 1934; Steinhardt, 1936; Blackwell, 1946; Aguilar & Stiles, 1954), have measured the differential threshold under a wide variety of conditions, and König & Brodhun's conclusions are substantially confirmed. The rise at high intensities was not found by Steinhardt except when there was no surround to the test patches of light, and the eye was consequently not adapted to the high intensities, but the question of a terminal rise in $\Delta I/I$ is now in some doubt again since Aguilar & Stiles (1954) have shown that it does undoubtedly occur under conditions when the rod mechanism alone is determining ΔI.

Stiles and his co-workers (Stiles & Crawford, 1933, 1934; Stiles, 1939, 1949; Flamant & Stiles, 1948) have introduced and developed the technique of using increment thresholds rather than difference thresholds: the incremental stimulus (ΔI) is superimposed on a large adapting field (I), and the subject's task is simply to detect the added stimulus. The principle result of this work has been to show, by varying the wave-lengths of background and incremental stimulus, how the over-all relation between ΔI and I can be resolved into almost independent components which are thought to belong to the rods and to the various types of cone. Each of these components shows a simpler relation between ΔI and I than the whole eye; there is a region where the intensity of the background has no influence on the increment threshold, joined by a short transitional section to a region where the increment threshold increases in direct proportion to the background intensity.

One might hope for an explanation of this simpler relation, but none has yet been forthcoming. The generalization made by Bouguer two centuries ago still stands, but it is only approximate, and it is completely empirical. Fechner's (1860) attempt to give it a theoretical backing was somewhat discredited when the experimental work which it provoked showed how inaccurate the generalization was. His idea that the absolute threshold is the limiting case of the differential threshold, with the 'Augenschwarz' taking the place of the background light, is clearly the precursor of the idea that intrinsic retinal noise limits absolute threshold (Hecht, 1945; Barlow, 1956). He also seems to have related thresholds to the scatter of values of a quantity representing, in the mind, the physical quantities being estimated or detected (see Finney, 1947); this is obviously the basis of the signal/noise discrimination theory of the nature of threshold, but Fechner postulated that the scatter was directly proportional to the magnitude of the physical quantity, whereas it is now clear that the natural postulate is that the scatter is proportional to the square root of the physical magnitude.

Hecht (1924, 1935) formulated a photochemical theory to account for the relation, but this must be discarded because the photosensitivity of the retinal pigments is lower than that required in his theory by several orders of magnitude, as pointed out by Baumgardt (1947), and de Vries (1943). Houstoun (1932) tried to account for the data by postulating that the thresholds of the visual receptors were spread throughout the whole working range of the eye, so that each threshold increment of intensity brought in a constant number of previously unexcited receptors. This theory requires that only a minute fraction of the receptors are able to respond to a threshold stimulus, which is hard to reconcile with the demonstration by Hecht *et al.* (1942) that not less than about 5 % of incident quanta participate in causing a threshold sensation.

More recently Rose (1942, 1948) and de Vries (1943, 1956) have pointed out that the general features of the relation between increment threshold and absolute intensity for the eye are similar to those for a photoelectric cell or a photographic plate. In the latter cases the basic limit is set by the statistical fluctuations in the number of quanta absorbed, and they suggest that the physiological mechanisms of the eye work so efficiently that the performance in this case too is close to the physical limit. Rose attempted to determine the 'quantum efficiency' (the fraction of quanta incident on the eye which are usefully employed by it in performing a set task) by comparing its performance with that of a photocell of known efficiency, and he went on to argue that it stayed constant over a wide range of background intensities and areas of test stimulus on the basis of calculations made from Blackwell's (1946) extensive data. His calculations are, however, open to the following criticisms. (1) In assessing quantum efficiency he does not seem to make due allowances for the known differences of sensitivity to different spectral lights. (2) His estimate of the signal/noise ratio of the human subject was only approximate. (3) Likewise his measure of the time over which the eye summated light was approximate, and he assumed that it was constant at a value of 0·2 sec both for the conditions of his experiment, and for all the conditions of Blackwell's experiments. De Vries (1956) based his acceptance of the fluctuation theory limit operating at human thresholds on the fact that $\Delta I \propto I^{\frac{1}{2}}$, and quotes Bouman (1952) for the validity of this law. It is not, however, clear, under what conditions ΔI is proportional to $I^{\frac{1}{2}}$, and when it is directly proportional to I. Aguilar & Stiles (1954) found big deviations from the behaviour expected according to fluctuation theory, and their very clear discussion casts some doubts on its usefulness in understanding psychophysical data.

Mueller (1950) considered various ways of incorporating quantum concepts in theories of intensity discrimination, and Tanner & Swets (1954) have given a very general treatment of thresholds as signal/noise discrimination problems, but neither piece of work shows close agreement between theoretical predictions and experimental results in the case of differential thresholds. Gregory & Cane (1955) have shown how Weber's law might result from 'neural noise' in the visual pathway, but Weber's law is not a good approximation to the truth at low intensities.

Rose & de Vries's theory would gain more general acceptance if the many parameters involved could be estimated, and if it could be shown that there is a range of conditions under which they stay constant.

According to the statistical laws governing the absorption of light quanta, when an average number of quanta equal to n are absorbed the fluctuations to be expected are proportional to $n^{\frac{1}{2}}$. If it is assumed that these fluctuations constitute 'noise' for the visual system and that the signal/noise ratio (or the fallibility of the response) is constant, then the number of additional quanta required from the 'signal' should also be proportional to $n^{\frac{1}{2}}$. Now it is certain that the concentration of rhodopsin does not vary appreciably over the range of intensities from threshold up to a level at least 10^6 above threshold, because the number of quanta of light absorbed in an exposure of moderate duration at this higher intensity is small compared with the total number of molecules of rhodopsin in the retina, and this conclusion is confirmed by measurements of the photosensitivity of rhodopsin in the retina (Rushton, 1956*a*). It is therefore reasonable to assume that the number of quanta absorbed is proportional to the quantity of light entering the eye over the whole of this range. Hence the threshold 'signal', ΔI, should be proportional to $I^{\frac{1}{2}}$ if the initial assumptions are correct.

The first aim of this paper was to test this prediction, and it is shown that '$\Delta I \propto I^{\frac{1}{2}}$' does hold over a certain range of conditions. The additional assumption that there is intrinsic noise in the visual pathway would account for ΔI levelling off at the absolute threshold, and the second aim was to find the value of this noise. It can be expressed in units of light intensity if one thinks of it as resulting from fluctuations in the quanta absorbed from an imaginary 'dark light' (cf. Fechner's 'Augenschwarz') which is always illuminating the retina in addition to any light actually entering the eye.

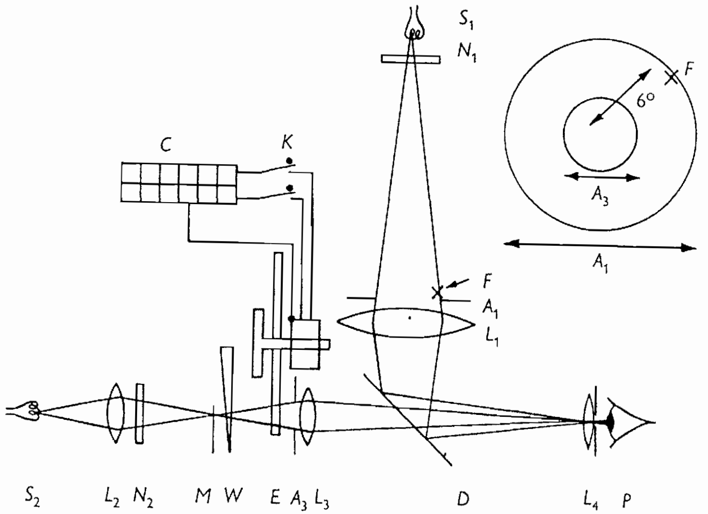

Fig. 1. Diagram of apparatus: explanation in text.

METHODS

Apparatus. The apparatus used in this and other experiments of this series is shown in Fig. 1. The two lamps S_1 and S_2 are under-run at a controlled voltage. The lens L_1 focuses the image of S_1 on to the artificial pupil P (2 mm in diameter) after reflexion in a glass plate D. L_2 focuses the image of S_2 on the blade of a moving armature shutter M; this shutter is controlled by electronic timing circuits. The light from S_2 then passes through a wedge W and one of a set of filters on a wheel at E. It is then collected by L_3 and an image of S_2 focused on the artificial pupil P. Aperture stops A_1 and A_3 delimit the background field and test field respectively as they are seen in Maxwellian view through P. A supplementary lens L_4 places the aperture A_3 in focus for the subject's eye. Additional neutral and colour filters can be placed in the pathways at N_1, N_2. A small red spot for fixation is provided at F, such that the centre of the test field falls 6° from the fovea in the inferior nasal quadrant. The appearance of the field to the subject's right eye is shown above the eye. The adapting field, limited by A_1, subtended 13° in all the experiments reported here.

The filters at E are mounted on a wheel on the shaft of a switch. This is wired through a 'Yes' and a 'No' key at K to a bank of six pairs of counters at C. The technique used for obtaining 'frequency of seeing' curves is described in another paper (Barlow, in preparation).

Calibration of filters and wedges. Ilford 'Spectral' filters were used to control the colour of the light, and for all experiments, except where otherwise stated, 603 (blue-green) was used in both background and test light. The transmission of the neutral filters was measured in a 'Uvispek' spectrophotometer at the dominant wave-length of the spectral filters. The wedge was then calibrated against these filters.

Calibration of intensity. A lamp calibrated by the National Physical Laboratory was run at an accurately controlled voltage and the light from it passed through a colour filter (Ilford 603) whose spectral transmission had been determined on a 'Uvispek' spectrophotometer. This fell on a piece of white card (reflectance assumed to be 80%) at a measured distance and normal to the incident light, and since the intensity and colour temperature of the standard were known, the spectral

distribution of energy in this light could be calculated. 85% of the energy lay between 480 and 510 mμ, and the peak was at 495 mμ. The white card was placed at an angle in front of L_3 (Fig. 1) and viewed through the artificial pupil P. In the centre of the card was a hole which passed light from L_3, and the intensity of this field, seen in Maxwellian view, was adjusted by the wedge W until its luminosity matched that of the card itself. The glass plate D was removed for this calibration, and transmission losses allowed for.

The quantities and intensities of light are expressed as the number of quanta of wave-length 507 mμ entering the eye (quanta/sec. degrees^2 for intensities) which would have had the same scotopic luminosity as the light which passed the exit pupil of the apparatus, using the scotopic luminosity function of Stiles & Smith (1944) to calculate the scotopic luminosities of the lights. Aguilar & Stiles (1954) calculated that $4{\cdot}46 \times 10^5$ quanta of 507 mμ/sec. degrees^2 produced a retinal illumination of 1 scotopic troland. This method of calibrating the absolute intensity of the lights was not adopted until late in the series of experiments. Before this, various intermediate standards were used, and the highest standard of absolute accuracy cannot be claimed.

Calibration of exposure durations. The light passing the shutter fell on a photocell and amplifier with a response time short compared with the duration of the exposure, and the output was displayed on a C.R.O. Opening and closing times were less than 1 msec, and the duration from half open to half closed was measured on the C.R.O. trace.

Subjects. Two subjects were used, the author and B.N., a technical assistant. Neither has any known abnormality of vision.

Thresholds. The subject's right eye was first completely dark-adapted. The subject then got in position on the apparatus by biting on a mould of his teeth and looked at the adapting field for a few minutes. The shutter was then set to open automatically about every 3 sec, and the subject moved the wedge until he was satisfied that the stimulus was just visible on the majority of occasions. Repeat determinations were made, care being taken that there was no tactile or other subsidiary clue as to the previous threshold setting. The standard error of such settings was estimated in an experiment in which thresholds were measured at 63 different combinations of area and duration of the stimulus spot. These thresholds were taken first in one order, then repeated in the reverse order, and the root mean square difference of repeat readings was 0·09 log. units, which gives a figure of 0·065 for the standard error of a single setting. The standard error of the thresholds shown in this paper should be less than this since they are the averages of two or four such settings. In some cases 'frequency of seeing' curves were done after thresholds had been determined in this way, and they showed that 'threshold' corresponded roughly to the 80% seen intensity. Though this self-setting technique of determining thresholds is doubtless less accurate than a method based on 'frequency of seeing' curves, it is very much quicker, since a reliable value can be obtained from 10 or 20 flashes taking only about a minute.

RESULTS

The effect of size and duration of stimulus on differential threshold

Fig. 2 shows an experiment in which the increment threshold was measured with three different types of test stimulus. The upper curve was obtained with a short (7·6 msec) duration, small (5·9 minutes diam.) stimulus; the middle with a long (940 msec) duration, small (5·9 minutes) stimulus; the lower with a long (940 msec) large (4·9°) stimulus. Log. increment threshold intensity (ΔI) is plotted against log. background (I); on this log.–log. plot with the background scale (abscissae) compressed relative to the ordinates the Weber–Fechner law ($\Delta I \propto I$) is represented by a line at about 63°, whereas the law predicted by the hypothesis that the increment threshold is limited by quantum fluctuations of the background is represented by a line at 45°. Weber's Law is a reasonable approximation for the results obtained with long, large, stimuli, especially at high intensities, but on the other hand the upper curve deviates strikingly from Weber's Law. This result suggests that the conditions most likely to yield the fluctuation theory law ($\Delta I \propto I^{\frac{1}{2}}$) would be short duration,

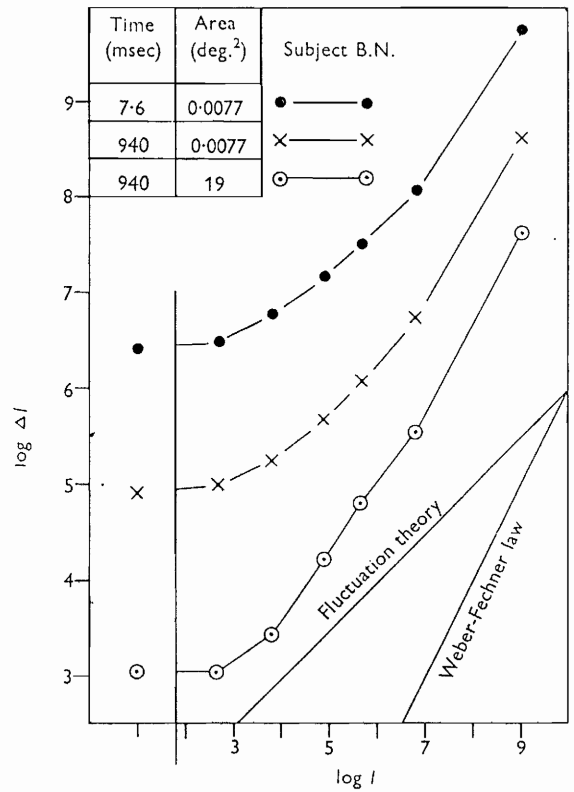

Fig. 2. Log. incremental threshold intensity (ΔI) plotted against log. background intensity (I) ●, for short duration small area; ×, for long duration small area; and ⊙, for long duration large area, test stimuli. Intensities in quanta (507 mμ)/sec. degrees². Lines indicate slopes predicted by Fluctuation theory and by Weber-Fechner Law.

small area, test stimuli superimposed upon backgrounds of moderately low intensity. More results were obtained from the other subject under these conditions, and they will be used for a closer comparison with a theoretical curve.

In Fig. 2 the three lines come closer together at the higher intensities of background light. Prolonging the duration of the stimulus to 1 sec and increasing its area to 20 sq. degrees bring about a smaller reduction in threshold intensity when the background is high than when it is low. The effect of the

background light, in fact, is to reduce the total amount of temporal and spatial summation in the range examined. These changes in summation are considered further elsewhere (Barlow, in preparation).

Comparison with theory

The theory that thresholds are limited by intrinsic retinal noise in total darkness, and by statistical fluctuations in the numbers of quanta absorbed when the stimulus is superimposed on a background, might provide an explanation for the case of a short duration, small area, test stimulus over a low intensity range of background brightnesses. The following theoretical formulation allows a more exact comparison between theory and experiment to be made. One assumption is implicit in the formulation, namely that 'intrinsic retinal noise' has an effect like an imaginary 'dark light' which gives an even illumination on the retina at all times, whether there is or is not a real background light entering the eye in addition. The validity of this assumption is considered further in the discussion; the justification at this point is that it leads to specific predictions about the relation between increment threshold and background intensity, and allots a unit of measurement to 'intrinsic retinal noise'.

Let ΔN = threshold incremental quantity of light in quanta entering the eye;
I = background intensity in quanta/sec. degrees² entering the eye;
X = 'dark light' causing intrinsic retinal noise (i.e. the intensity of background which, because of the inevitable fluctuations in the number of absorbed quanta, would have the same effect on the increment threshold as the intrinsic retinal noise itself);
F = fraction of quanta incident at the cornea (or fraction of X) which are effectively absorbed;
α = area of the retina over which light from the background (or the retinal noise) is liable to be confused with the test stimulus;
τ = duration of time during which light of the background is liable to be confused with the stimulus;
K = reliability factor or signal/noise ratio of threshold responses.

Of these quantities only the first two are directly determined by experiment; the remaining five are unknown parameters required by the theory.

The mean number of events liable to be confused with the effective absorption of a quantum of light from the stimulus, but occurring without a stimulus, is $F\alpha\tau(I+X)$. The Poisson distribution will be followed, but if the number is fairly large a normal distribution of standard deviation equal to the square root of the mean is a reasonable approximation. The number of quanta effectively absorbed from the stimulus flash at threshold is $F\Delta N$, and according to the hypothesis this is a certain multiple, K, times the standard deviation in the number of background events. Therefore

$$F.\Delta N = K(F\alpha\tau(I+X))^{\frac{1}{2}},$$

which reduces to

$$\Delta N = (I+X)^{\frac{1}{2}}.K(\alpha\tau/F)^{\frac{1}{2}}, \qquad (1)$$

in which the right-hand side is divided into a term containing X, which we can try to estimate from the present experiment, and a term containing four other parameters: it is possible to get a value for the whole of this term, which can therefore be treated as a single lumped parameter.

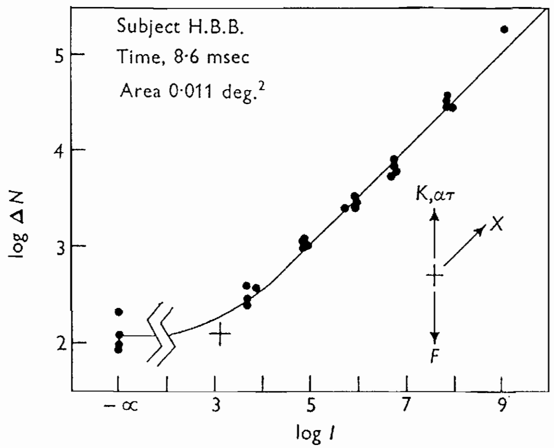

Fig. 3. Log. increment threshold quantity of light (ΔN) plotted against log. background intensity (I). Four determinations on one subject. Stimulus short duration, small area. Thresholds in number of quanta of 507 mμ at the cornea; background intensity in quanta/sec. degrees². Solid line is theoretical curve for $\Delta N = K(\alpha\tau/F)^{\frac{1}{2}}.\ (I+X)^{\frac{1}{2}}$ for $K(\alpha\tau/F)^{\frac{1}{2}} = 3{\cdot}3$, $X = 1260$. + shows point of intersection of horizontal and slanting asymptotes of theoretical line, and in the bottom right corner arrows show how this point, and with it the whole theoretical curve, is displaced by increases of the different parameters.

Assuming that all the parameters stay constant, one can calculate predicted values for the increment threshold from this formula. In Fig. 3 the continuous line is such a curve plotted on log.–log. co-ordinates. The dots are experimental values of the increment threshold using a short (8·6 msec) small (0·011 sq.degrees) test stimulus. One subject was used, and a set of paired threshold determinations was done in ascending and descending order of background brightness. The average of these four settings at each background intensity is plotted as a single dot. The whole procedure was repeated four times, three being within one week, and the fourth (slightly different abscissa values) four months later. It is clear that the agreement between the theoretical curve and the experimental points is good over this range of background intensities. The single determination at the highest background brightness is not far from the line, but other experiments showed that there was a consistent tendency for the experimental values to be higher than the predicted values at these brightnesses; they are, however, about 10^5 or 10^6 times the threshold intensity for the adapting field.

It might be thought that the five separate parameters of the theory would make it easy to fit a theoretical curve to the points, but it was assumed that the parameters were constant; with this method of plotting, the curve is shifted vertically or diagonally, but is not altered in shape when their values are changed. There are therefore only two degrees of freedom in fitting the curve to the points. As shown by the arrows in Fig. 3, a change in any of the four parameters F, α, τ, K, produces a vertical displacement of the theoretical curve, whereas a change in X moves it diagonally. Fitting the curve consequently gives unique values for X and the term $K(\alpha\tau/F)^{\frac{1}{2}}$. The value for X is easily found, for it is the value of I at the point where the horizontal and slanting asymptotes of the theoretical curve meet. In this case, $\log I = 3{\cdot}1$, at this point, so $X = 1260$ quanta/sec. degrees², that is to say the retinal noise is equal to the quantum fluctuations to be expected from a field of this intensity. The value of the other, lumped, parameter can be found by substitution in the formula (1), and this gives

$$K(\alpha\tau/F)^{\frac{1}{2}} = 3{\cdot}3.$$

By the same method parameters can be found for the other subject from the experiment shown in Fig. 2. In this case $X = 2500$ quanta/sec. degrees², and $K(\alpha\tau/F)^{\frac{1}{2}} = 2{\cdot}95$.

Other estimates of intrinsic retinal noise

The principle of the above determination of retinal noise is, first, to establish the law relating increment threshold to background intensity over a range where background noise contributes a negligible amount to the total noise, then to extrapolate this law to zero background intensity where retinal noise forms all the background noise. It is, in fact, the same principle as Fechner suggested should be used to determine the 'Augenschwarz' or dark light of the eye, and Volkmann (quoted in Fechner, 1860) and König & Brodhun (König, 1903) did in fact make estimates by this method. Volkmann assumed that $\Delta I/I$ had a value of 0·01 and that it stayed constant down to absolute threshold; consequently he obtained a very high value for the dark light (equivalent to the luminance of black velvet lit by a candle at a distance of 9 feet), and Gregory & Cane (1955) who used a similar method, also obtained a high value. König & Brodhun (König, 1903), on the other hand, realized that $\Delta I/I$ increased in value as the absolute intensity decreased, and argued that the dark light was equal to the absolute threshold intensity; this gives a value close to that derived from their data below, though the argument used here is not quite the same as theirs. The difference between the method suggested by Fechner and that used in this paper lies in the law established for the behaviour of the increment threshold, and the reason for this difference depends upon the use of different sizes and durations of test stimulus, and different ranges of background brightnesses. The square root law ($\Delta I \propto I^{\frac{1}{2}}$) inspires special confidence because it is based on statistical theory, but there is independent justification for regarding the absolute threshold as the limit of the differential threshold set by the dark light of the eye, and deriving its value by extrapolating *any* law relating increment threshold and background intensity at low intensities. Now if one looks at Fig. 2, it will be seen that, to a first approximation, the curves for different types of stimulus start to turn upwards at the same value of background intensity. They differ in the slope of their rising portions, and a general approximate law seems to be that the increment threshold varies as some power of the background intensity; this power varies between 0·5 and 1, but stays constant for any set of conditions over a moderate range just above the absolute threshold. Such a simple power law is represented by a straight line on the plot of log ΔI against log I, and the noise level is very easily found by the intersection of this line with the ordinate corresponding to the absolute threshold for the test stimulus; the abscissa at this point is the background intensity which is equivalent to the dark light.

Table 1 shows some values for the dark light obtained in this way from the literature, together with the results of the present experiments. At the bottom of the table are some values for H. B. and B. N. obtained with a variety of different test stimuli. It will be seen that the value of X obtained does not depend in a systematic way upon the type of test stimulus used, even though this does affect the power of I in the approximation which has been extrapolated. The same is true of the figures derived from Blackwell's data for the largest and smallest size of test field he used. This confirms that curves of the type shown in Figs. 2 and 3, although they differ in the slopes of their rising portions, always turn upwards at about the same background intensity. This fact is some additional justification for applying the power law extrapolation to other data, even though the law is an empirical one except for the case of the short, small stimulus. The only figures which were derived from the literature with complete confidence were those of Aguilar & Stiles, and it will be seen that the values obtained were of the same order of magnitude as those of the two subjects of this paper. The absolute values derived from König & Brodhun, Blanchard and Blackwell are unreliable for the reasons given in the footnotes to the table.

Fitting the theoretical curve to the experimental points in Fig. 3 gave values for two parameters. The lumped parameter $K(\alpha\tau/F)^{\frac{1}{2}}$ fixes the position of the sloping asymptote of the theoretical curve, and the values obtained for the two subjects of this paper agreed well with each other. The noise level, X, fixes the position at which the theoretical curve deviates from the slanting asymptote and levels out to the value of the absolute threshold, and this value differed by

a factor of about 2 between the two subjects. The values in the table show the same great variability of X from subject to subject, even when one only compares figures obtained under identical conditions. Brodhun's dark light is about 6 times König's, and Aguilar & Stiles's subject D has about 6 times the dark light of their subject A. In view of this big variability in X, it was striking that the sloping parts of the curves of log ΔI against log I, were almost exactly superimposable for König & Brodhun, and also for Aguilar & Stiles's subjects. The lumped parameter which fixes the position of the sloping portion of the curve seems to show relatively little variability from person to person.

TABLE 1. Values of noise level, expressed as a light intensity, derived from various authors

Author	Subject	Conditions of determination	msec	Diam.	Power law extra-polated	Dark light: Quanta (507) / sec. degrees²	Dark light: Scotopic trolands
Konig* & Brodhun	K	Adjacent rectangles 3° × 4⅓° at I and $I + \Delta I$ exposed continuously. λ = 505 mμ. One eye. No fixation			0·7	2,500	0·0056
	B†				0·8	16,000	0·036
Blanchard‡§	—	Rectangles 2½° × 5°. White light. Otherwise as above			0·55	500	0·0011
Blackwell§	Nineteen young girls	Disk 2° or 3·6′ added to large field, exposed for 6 sec in one of 8 positions. White light. Both eyes		2°	0·63	5,250	0·012
				3·6′	0·5	6,000	0·013
Aguilar & Stiles	A	9° disk added to 20° field in 0·2 sec exposures. Centred 9° from fovea. One eye. Green test light; red field			0·93	200	0·00045
	B				0·92	1,000	0·0022
	C				0·87	700	0·0016
	D				0·99	1,300	0·0029
Barlow	H.B.	Stimulus added to centre of 12° field 6° from the fovea. One eye. Blue-green light	8·6	7·1′	0·5	1,300	0·0029
			945	7·1′	0·55	630	0·0014
			945	5·9°	0·75	1,000	0·0022
	B.N.		7·6	5·9′	0·5	2,500	0·0056
			935	5·9′	0·6	3,200	0·0072
			935	4·9°	0·75	2,500	0·0056

* Diameter of exit pupil of apparatus uncertain; I have followed Hecht (1924) in assuming that it was n limiting.

† Brodhun was a deuteranope.

‡ Value of absolute threshold is rather uncertain; I have used a figure from his paper obtained under cond tions not quite identical with those of the differential threshold measurements.

§ Temperature of white light source used not specified, hence scotopic luminosities uncertain: I have assum 2848° K.

DISCUSSION

There are three aspects of this work to be discussed. First is the question of the extent to which these results support the hypothesis that visual thresholds are efficient statistical judgements of constant fallibility, the limiting factor being the quantum fluctuations of the background light in the case of the differential threshold, and intrinsic retinal noise in the case of the absolute threshold. Second is the question of the choice of a unit to measure the retinal noise, the values that are found, and the values of the other parameters. Finally there is the question whether the values found for the retinal noise are compatible with other results.

Visual thresholds as statistical judgements

It has been shown elsewhere (Barlow, 1956) that the idea that absolute threshold is a signal/noise discrimination is entirely compatible with the data for absolute threshold, and explains some aspects not accounted for on other hypotheses; the actual value of the noise is considered later. The fact that a background light usually increases the threshold is an additional argument in favour of this explanation, since alternative hypotheses might lead one to expect that a background light would decrease the threshold by 'priming' the system; if, say, 5 rods must be activated before the resulting nervous activity is great enough to cause a sensation, then one might expect a background which activated an average of, say, 2 rods to reduce the threshold intensity to 3/5 of its former value. This naïve idea is certainly wrong, but the matter is confused by the fact that background lights have sometimes been reported to reduce the threshold for a superimposed stimulus instead of increasing it. Few thresholds were determined in the relevant range in this series of experiments, but the matter was rather fully studied by Stiles & Crawford (1934), and in the only case where they found the effect they attributed it to failure of the eye to accommodate when the background intensities were weak.

When the intensity of a background light is reduced there comes a point at which it no longer has any influence on the threshold of a stimulus superimposed upon it. The interpretation put on this here is that the internal noise in the visual system becomes the limiting noise when the fluctuations from the background are reduced below a certain point. Mueller (1950) offers an entirely different explanation for it which does not require intrinsic retinal noise and must therefore be carefully considered. He criticizes the formula $\Delta I \propto I^{\frac{1}{2}}$ for the relation between increment threshold and background intensity on the grounds that it only takes account of the fluctuations of the background (I) and neglects the fluctuations of the stimulus light ($I+\Delta I$). He proposes instead the formula $\Delta I \propto (2I+\Delta I)^{\frac{1}{2}}$, which is based on the idea that the difference between the number of quanta absorbed from the background and the number absorbed from the stimulus light ($I+\Delta I$) must lie outside the normal range of variation of this difference before the two lights can be distinguished from each other reliably. 'Reliably' must mean that the subject only rarely claims that $I+\Delta I$ is greater than I when ΔI is actually zero (i.e. there are few false positives), and also that he rarely fails to say $I+\Delta I$ is the greater when ΔI has threshold value (few false negative responses). Now these two types of error are really quite distinct, and it is hard to justify lumping them together in this way. A particular objection might be raised in the case where I is reduced to zero, for if there is no noise the possibility of false positive responses vanishes; the meaning of 'reliably' has changed slightly because the subject is exposed to different errors. In this situation the implication of Mueller's treatment is that a stimulus would be reliably detected if the probability of zero quanta being absorbed from it is low. No explanation is given for the fact that 5 or more quanta must be absorbed before a stimulus is seen (Hecht *et al.* 1942).

It may help at this point to consider the formula $\Delta I = K_1 I^{\frac{1}{2}} + K_2 (I+\Delta I)^{\frac{1}{2}}$; like Mueller's formula this takes account of fluctuations of both lights, but unlike his it distinguishes between them and contains two constants (K_1 and K_2) to represent their frequencies. Fig. 4 illustrates how it is obtained. The three histograms are Poisson distributions showing the frequency with which different numbers of quanta are absorbed at three different light intensities. If the intensity for the uppermost histogram is I (expressed here in quanta absorbed), and one knows the frequency with which the subject gives false positive responses to a blank stimulus ($\Delta I = 0$), the vertical line separating 'seen' from 'not seen' can be drawn so that it divides this distribution in the appropriate ratio. K_1 is the deviate from the mean which divides a normal distribution of standard deviation unity in this same ratio, so that this line is at approximately $I + K_1 I^{\frac{1}{2}}$. Adding ΔI to I shifts the distribution to the right and increases the proportion of 'seen' responses; suppose that ΔI is at an intensity such that about 55 % are seen, then the vertical line must lie close to the median of the distribution, as shown in the middle histogram. This means that $I+\Delta I = I + K_1 I^{\frac{1}{2}}$; hence $\Delta I = K_1 I^{\frac{1}{2}}$ and K_2 is close to zero. This is the justification for using the simple square root law in this paper, and it is not seriously affected by the fact that the intensity chosen for threshold corresponded to about 80 % 'seen' responses: it is

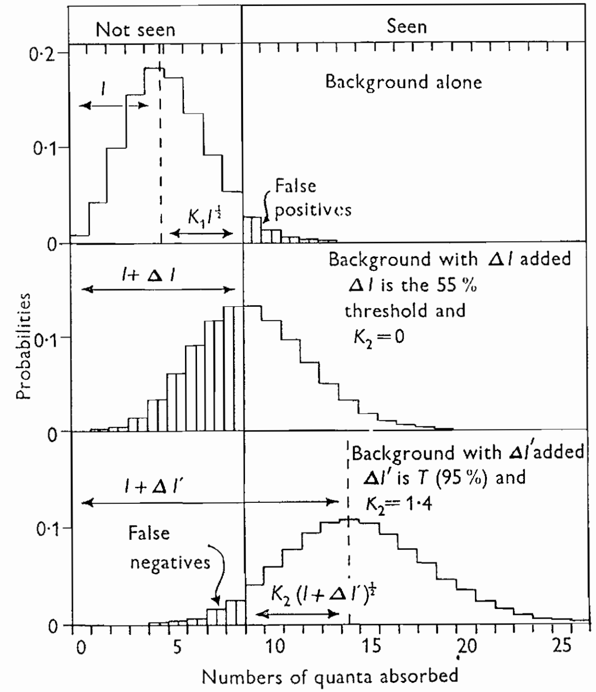

Fig. 4. Diagram to show the basis for the approximate formula $\Delta I = K_1 I^{\frac{1}{2}} + K_2 (I+\Delta I)^{\frac{1}{2}}$. The top histogram shows the distribution of quanta absorbed from the background alone; it is a Poisson distribution for an average of 4·7 quanta absorbed; the probability of 9 or more quanta being absorbed is 0·05, so if 5 % false possitives are allowed the critical number of quanta which must be exceeded to obtain a 'seen' response is 9, and $K_1 = 2$. The middle normogram shows the distribution of quanta absorbed when a stimulus (ΔI) is added to the background; 9 or more quanta are absorbed on 55 % of occasions, and this would usually be taken as threshold; for this definition of threshold $K_2 = 0$. The lower histogram shows the distribution of quanta absorbed when a stronger stimulus ($\Delta I'$), which the subject fails to detect on only 5 % of occasions, is added to the background; for this definition of threshold $K_2 = 1·4$. If the numbers of quanta absorbed were larger, or if the distributions were normal, $K_1 = K_2 = 1·64$ if there are 5 % of false positive and 5 % of false negative responses.

possible to calculate corrections from 'frequency of seeing' curves, and they do not greatly affect the values obtained for the dark light of the eye. The situation shown in the lowest histogram must be closer to that considered by Mueller; it corresponds to 95 % of stimuli 'seen', and requires an increase of ΔI by $K_2(I+\Delta I)^{\frac{1}{2}}$ beyond the value it had in the centre histogram; hence $\Delta I' = K_1 I^{\frac{1}{2}} + K_2(I+\Delta I')^{\frac{1}{2}}$. The fluctuations of the background light (I) are important in avoiding false positives but it is only when the test light ($I+\Delta I$) has to be bright enough for the subject to avoid false negatives also that the fluctuations of the stimulus light have to be considered.

The hypothesis that thresholds are statistical judgements of constant fallibility predicts the relationship $\Delta I \propto I^{\frac{1}{2}}$, and this has been found to hold under the following conditions. First, the intensity of the background must be between about 10^4 and 10^8 quanta (507 mμ)/sec. degrees^2 (2×10^{-2} to 2×10^2 scotopic trolands). The lower limit is set, according to the arguments given above, by the noise of the background light dropping below the intrinsic noise. It is not certain what sets the upper limit, but it is not far short of the point at which Aguilar & Stiles found that the rod mechanism began to be saturated. The breakdown of the square root law may be connected with this phenomenon, but in the present experiments it is not certain that the rods are determining threshold at the upper end of the range considered. An attempt was made to check this point by a method similar to that of Flamant & Stiles (1948). First the background of blue-green light was set at an intensity of 6×10^6 quanta/sec. degrees^2 (11 scotopic trolands), and the superimposed stimulus (short duration, small area) adjusted to threshold value; the colour of the background was then changed by using the other Ilford spectral filters in the background pathway in place of the blue-green, and it was found that for each colour the energy required to make the stimulus continue to be threshold followed the scotopic luminosity function. It is therefore probable that rods were determining the threshold up to this value of the background, but it is not certain that they were at higher values.

The relation $\Delta I \propto I^{\frac{1}{2}}$ has not always been found to hold even over the appropriate low range of background intensities (see tabulated figures for the slope of the linear part of plots of log ΔI against log I), but it does seem to hold for test stimuli of small area and short duration added to a large adapting field. This is shown in Figs. 2 and 3, and has also been found by other workers. In the table it is seen that Blackwell found it for a small test field, even though the duration of the exposure was not short, and Blanchard's results lie close to it even though he used large test areas. Both Stiles & Crawford (1934) and Bouman (1952) found that the area and duration of the test area had an effect on the relation between differential threshold and background intensity, and under some conditions their results approximate to $\Delta I \propto I^{\frac{1}{2}}$. More results are available which show how temporal and spatial summation changes when the background brightness changes (Barlow, in preparation), and an explanation for the increased spatial summation at low background brightnesses is possibly provided by the disappearance of lateral inhibition at low intensities that has been shown to occur in the cat's retina (Barlow, FitzHugh & Kuffler, 1957).

The fact that the square root law does hold, even though it is only for a special type of test stimulus and over a moderate range of backgrounds, clearly encourages one to pursue the idea that thresholds are statistical judgements.

Choice of unit for retinal noise and values of parameters

The first step in the quantitative approach is to justify the choice of a unit to measure the retinal noise. Following the idea that it is related to Fechner's 'Augenschwarz', or the dark light of the eye, it is here expressed in units of light intensity. Thus if it is said that the dark light has a certain value, this means that a light of this intensity entering the eye would by itself cause the same amount of noise in the visual system that it is deduced to have in total darkness. This unit is derived from the experimental measurements very directly, which is a strong reason for choosing it, but it is in some ways both an odd and an arbitrary choice. It is odd because the actual amount of noise will vary as the square root of the intensity expressed in this unit, but as long as this is realized it is not of great importance. It is arbitrary because it leads one to expect that the noise will behave in every way like a uniform background of this intensity, and it has not been proved that this is so.

The choice of a unit is connected with one's idea of the actual source of the noise, and a factor influencing the present choice was the view that the noise may result from thermal breakdown of visual purple, since this would behave very much like a dim illumination of the retina. Some of the complexities of the problem will be seen, however, if one considers the contrasting hypothesis that noise is caused by random processes later on in the chain of events which ends in the subject either seeing or not seeing the stimulus. We may suppose that the magnitude of a quantity in the brain resulting from a given stimulus is fixed in a rigid determinate way, except for the inevitable fluctuations resulting from the quantal structure of the light; whether the stimulus is detected or not depends upon whether the magnitude of this quantity exceeds a certain threshold value, and noise can be introduced by supposing that this threshold value fluctuates in a random manner. Hecht *et al.* (1942), and Pirenne & Marriott (1955), have considered this type of noise, and Marriott (1956) has shown that it will produce effects similar in some ways to the spontaneous decomposition of visual purple. Now if this was the cause of noise it might be very awkward to express it in terms of a light intensity. It would, however, be equally awkward to explain the results of Fig. 2 and the bottom figures of the table in terms of this theory, for without making additional assumptions there is no reason why the apparent noise level for different types of test stimulus should always have approximately the same value when expressed in units of light intensity. Likewise, Piper's Law (threshold intensity inversely proportional to square root of stimulus area) seems natural if noise is uniformly spread over the retina, but additional assumptions are required to account for it if noise occurs later in the visual system. For these reasons it is at least convenient to express noise as 'dark light', and the next step is to decide its intensity.

Stiles & Aguilar's four subjects and the two of this paper gave values ranging between 200 and 3200 quanta (507)/sec. degrees^2, or between 0·00045 and 0·0072 scotopic trolands. It is likely that more subjects would give an even wider scatter, but as a value to discuss 1000 quanta/sec. degrees^2, or 0·0022 scotopic trolands, might be taken, bearing in mind that it can drop as low as 1/5 and can rise to three times this value.

The values of the lumped parameter $K(\alpha\tau/F)^{\frac{1}{2}}$ were 3·3 and 2·95 for the two subjects of this experiment. The values of the component parameters will be discussed elsewhere, but it is worth commenting on the good agreement between the two subjects for the value of this parameter which contrasts with the rather big differences between their retinal noise levels. Likewise, it was found when preparing Table 1 that results obtained by different subjects under identical conditions tended to agree well for the differential thresholds, but varied widely for the absolute thresholds.

Dark light and the sensitivity of the eye

It will naturally be asked whether the noise levels that have been arrived at are compatible with the extreme sensitivity of the eye. The first point to be made concerns the extreme variability of noise level in different subjects compared with the relative uniformity of differential thresholds; it appears that individuals with unusually high or low values for their absolute thresholds do not have correspondingly high or low values for their difference thresholds. This is what one would expect if the high or low absolute thresholds were actually caused by high or low levels of dark light or retinal noise. Pirenne (1956) reviewed the literature on absolute thresholds, and concluded that they might differ by a factor of 5 amongst young subjects in good health, and it seems possible that a large part of this variability is to be attributed to differences of dark light.

In a previous paper (Barlow, 1956) it was shown that the data of Hecht *et al.* on absolute threshold allowed one to calculate an upper limit to the permissible noise level, and this limit was strongly dependent on the fraction of quanta striking the cornea which were effectively absorbed by the rods. Taking the value of 0·1 (Rushton, 1956*b*) for this fraction, the upper limit for the noise according to that paper was equivalent to that resulting from the occurrence of an average of 9·7 random events confusable with the events following the effective absorption of a quantum of light from the stimulus. To convert this into a unit of light intensity, one must know the area and time over which these

events must occur in order to be confusable with the light from the stimulus. If these are identified with the area and time over which the eye is able to integrate light completely, one can, provisionally, use Graham & Margaria's (1935) figures of 1 sq. degree and 0·1 sec. This gives a permissible noise level equivalent to that resulting from the effective absorption of 97 quanta/sec. degrees^2, or an external light intensity sending 970 quanta/sec. degrees^2 into the eye; this is close to the level of dark light arrived at in this paper. The various quantities which are required are not known with sufficient accuracy for one to have very much confidence in this calculation, but it is included to show that the result of this paper is reconcilable with the known values of the absolute threshold for a short small stimulus and with Rushton's recent estimate of the fraction of quanta absorbed. Similarly, the figures for the retinal noise obtained here are below the upper limits calculated by Denton & Pirenne (1954) and are consistent with the low values of absolute threshold found by them for large fields exposed for long durations.

Maintained discharge of retinal ganglion cells

It has been shown that the ganglion cells of the cat's retina discharge impulses in an irregular, apparently random manner even when the eye is in total darkness (Kuffler, FitzHugh & Barlow, 1957), and the question naturally arises whether such a discharge fits in with values for the dark light found here. There is not very much information on the visual performance of the cat, but what there is suggests that its retina has approximately the same sensitivity as that of the human, the differences in over-all performance resulting from the different apertures of the optical systems of the two eyes and the presence of a reflecting tapetum in the cat (see Pirenne, 1956). Let us then ask the question: 'Would a ganglion cell in the human retina which was discharging like those of the cat's retina, and which picked up from a receptive field of the same dimensions as those of the cat's retina, be compatible with the known sensitivity of the human eye?' The results of this paper suggest that the noise from a light sending into the eye 1000 quanta/sec. degrees^2 can be tolerated. One must make an assumption about the relation between the number of quanta absorbed and the number of impulses that result in order to decide whether the observed noise of ganglion cells is greater or less than this. The distribution of impulse intervals found by Kuffler *et al.* (1957) was approximately what would result if one impulse was produced when 5 (or rather less) quanta were absorbed, and the mean impulse rate was rarely as high as 50/sec in the dark-adapted eye. These figures would point to the absorption of 250 quanta/sec, or, if 0·1 are absorbed, they point to a dark light causing 2500 quanta to fall in a receptive field per second. The receptive fields of a large ganglion cell of the cat's eye would subtend about 10 square degrees if placed in the human eye, so the dark light calculated from the discharges of these ganglion cells is about

250 quanta/sec. degrees². Since this is at the lower end of the range of dark lights found in this paper it may be concluded that, if an impulse from a ganglion cell of the cat's retina can be produced by the absorption of 5 quanta or less, then the noise of the maintained discharge does not exceed the limit worked out from figures for the performance of the human eye.

General conclusion

The form of the relation between background intensity and the threshold for a short duration, small area, incremental stimulus agrees with that predicted from the following hypothesis: human thresholds are efficient statistical judgements of constant fallibility in which 'noise'—the random factor which tends to cause errors—arises from fluctuations in the number of quanta absorbed from the background light and the 'dark light'. To this extent the hypothesis is supported, but two important questions are left unanswered: first, can the quantities F, α, τ, and K (see p. 475) be estimated by independent experiments, and if so does the value of $K(\alpha\tau/F)^{\frac{1}{2}}$ agree with that found here? And secondly, can reasons be found for the departures from the theoretical predictions which occur when the test stimulus is of long duration or large area, and when the background intensity is high?

SUMMARY

1. It has been suggested that visual thresholds are efficient statistical judgements of constant fallibility; the differential sensitivity of the eye is limited by fluctuations in the number of quanta absorbed from the background light, and the absolute sensitivity by fluctuations in the dark light of the eye, according to this hypothesis.

2. The increment threshold of the eye at low background intensities has been determined in blue-green light with stimuli of different areas and durations, and the results compared with those predicted by the above hypothesis.

3. The results fit the theoretical predictions for the case of stimuli of short duration and small area (against a background of large area) for a range of background intensities up to about 10 scotopic trolands.

4. There are big discrepancies between theoretical and observed values of increment threshold when the stimulus is large and exposed for long durations.

5. The amount of spatial and temporal summation is decreased as the background intensity is raised.

6. From the agreement in 3 (above) it is calculated that the dark light of the human eye has a value approximately equal to that of a light sending into the eye 1000 quanta (507 mμ)/sec. degrees² (0·0022 scotopic trolands). It is very variable from subject to subject, ranging from about 1/5 to 3 times this value.

7. These conclusions are compared with figures for the dark light calculated from the literature, and are shown to be compatible with the extreme

sensitivity of the human eye to short duration, small area, stimuli and to large stimuli exposed for long durations. The random irregular discharge of impulses from ganglion cells of the cat's retina is also compatible with extreme sensitivity provided that one impulse can be caused by the absorption of less than 5 quanta.

8. The fit of 3 (above) also allows one to calculate the value of a lumped parameter dependent on the fraction of quanta incident on the pupil which are effectively absorbed by rods, upon the area of retina and duration of time for which these absorptions are liable to be confused with absorptions of quanta from the stimulus light, and upon the reliability factor, or degree of fallibility, of the threshold judgement. This quantity appears to vary less from individual to individual than does the dark light.

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