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MEASUREMENTS OF THE QUANTUM EFFICIENCY OF DISCRIMINATION IN HUMAN SCOTOPIC VISION

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In the previous paper (Barlow, 1962) a method for determining the quantum efficiency of vision was described. In the present paper some results obtained on human parafoveal scotopic vision are reported.

There are many experimental parameters involved in an estimate of overall quantum efficiency: for the stimulus these are the area, duration, intensity, retinal location, colour, and the relative intensity of the pair of stimuli. Since it is here the ability to discriminate two stimuli which is being used to estimate efficiency, one is not restricted to intensities lying close to threshold, so that an additional stimulus variable is introduced—one which turns out to be important. There are further variables associated with the state of adaptation of the eye. It would be a formidable task to investigate the effects of each variable, and rather a futile one when so much is already known about the effects of each upon the threshold. The experiments reported here were intended primarily to confirm that the highest attainable figure for quantum efficiency is in the neighbourhood of 5 %, and to find whether this high figure can be maintained when the eye is light-adapted. Exploratory observations are reported indicating that, in any given conditions, the highest efficiencies are obtained when discriminating between intensities near to the subjective threshold. It is also shown that light adaptation shifts to higher intensities the range where discrimination is most efficient.

METHODS

Optical. The optical apparatus was built along conventional lines and an essentially similar form has been described before (Barlow, 1957). Calibration was done by using a photon multiplier to compare the output of the apparatus with that of a lamp standardized by the N.P.L. These lights had both passed through a fairly narrow band green filter (Ilford 604), and were of very similar spectral composition: the fact that the photon multiplier has a spectral sensitivity different from that of the eye is therefore unimportant. The main calibrations were made with standard and unknown lights nearly equal to each other in intensity so that possible non-linearity of photocell output is also unimportant. Further, they were done at an intensity near to that required by the eye at absolute threshold, the attenuation of the standard being achieved by increasing its distance. Errors of calibration of wedges and screens therefore had the least effect at low intensities, where quantum efficiencies are high and their accurate determination of most interest.

From the known spectral composition of the standard it was possible to calculate the number of quanta per second per square degree of wave-length 507 mμ that would have had the same scotopic luminosity. All light intensities are expressed in these units: they can be converted into scotopic trolands by dividing by $4{\cdot}46 \times 10^5$ (Aguilar & Stiles, 1954). The orange background light used in the type of experiment shown in Fig. 3 was calibrated by scotopic matching (using the peripheral retina at very low luminance), the screens and wedges being recalibrated for orange light. The glow modulator tube used in the experiments shown in Fig. 1 was also calibrated visually.

The shutter was a simple rotating sector actuated by a spring or weight, and released by the subject pushing it gently over top dead centre. Calibrations showed that the exposure was reproducible both over a short term and a long term.

Counters, etc. The device for giving brighter or dimmer stimuli and counting responses was based upon a telephone-type key switch operated by a pair of solenoids. Upon its key was mounted a filter of the desired density (usually about 0·3), and this was pushed into or out of the optical path by the solenoids. The current for these came from a 3-position key switch operated by the subject. In its upper position the filter was out and in its lower position it was in, so that the subject could deliver to himself brighter or dimmer flashes as desired. In the central position the current was switched through a bistable relay: this relay was kept buzzing at 50 c/s as long as the subject's key switch was away from the central position; therefore when this switch was placed in the centre position the relay stopped in one or other position, the current was switched to one or other of the solenoids, and the filter was moved into or out of the optical path. It was necessary, but not easy, to ensure that these solenoids operated silently and without jerks which might give the subject consciously or unconsciously utilized clues as to which way the filter had moved. The bistable relay was adjusted to give brighter and dimmer stimuli with nearly equal frequency, and no evidence of sequential tendencies was found.

The subject had a second 3-position key switch with which to signal his answers. He pushed it up when he thought the unknown was one of the brighter stimuli, down when he thought it was one of the dimmer. Four counters were wired up through the solenoid-operated, filter-bearing switch and the subject's response switch, and counted separately each of the four possible combinations of bright or dim stimulus with bright or dim response.

Procedure. The exact procedure varied. Sometimes (Procedure 1) the subject selected and delivered to his eye brighter or dimmer flashes as often as he liked up to the moment when he gave himself an unknown, and again after he had classified this flash; sometimes (Procedure 2) he gave himself a regular sequence of brighter, dimmer, unknown, omitting the first ten or twenty counts while he established his criterion; and sometimes (Procedure 3) he gave himself no known stimuli, simply classifying the unknowns according to whether he saw them or not. In all cases a brief explanation of the nature of the test was given to the subject, and he was told that he must classify each unknown before seeing another known. This forced-choice procedure did not seem to cause any difficulty, possibly because subjects understood that they were bound to make some false classifications.

RESULTS

Highest values of overall quantum efficiency (F)

The first five entries in Table 1 were obtained on subjects who were completely dark-adapted and were fixating a weak red light so that the stimulus lay 15° from the fovea in the nasal field. The subject worked the shutter and controlled the moment of release. These are the conditions which yield the lowest threshold for a short-duration, small-area stimulus. In the first four cases the subject could also select and deliver to his eye flashes of intensity M_1 or M_2 as often as he liked up to the moment when he gave himself an unknown flash, and again after he had classified this flash (Procedure 1). The intensities chosen for the stimuli were close to threshold, the procedure being for the subject to adjust the intensity himself until he could 'just see it' on the majority of trials. The average of several such settings was taken, and then the apparatus was left so that the lower of the two flashes was at this level, the upper being about double. The subject could interrupt the series of some 100 unknown flashes at any time if he wanted a rest. The first subject (the author) was experienced at the task, the other three inexperienced. R.W. was an undergraduate doing his second session as subject: J. R. and P.M. were research workers accustomed to psychophysical experimentation, but doing this particular experiment for the first time. The stimulus area and duration for the first

TABLE 1. Overall quantum efficiencies of discrimination of stimuli of near-threshold intensity. Procedures are 1, 2, 3, described in the text. S_1, S_2, the brighter and dimmer stimuli. r_1, r_2, the numbers of each classed as brighter. n_1, n_2, the total numbers of each presented. The first five entries are determinations made on four subjects under conditions that yield the highest efficiency. The second five are all the determinations made on one subject on one day, and show that changing the ratio of intensities of the pair of stimuli has little effect on the value of the estimate, but does affect the calculated accuracy. The third five are the first determinations made on a new subject, indicating that great skill and experience are not required for the two-point method. The standard deviations given after each determination were calculated as previously described, and may be inaccurate because n is small (Barlow, 1961). Those given after the means are standard deviations of the determinations, calculated from the experimental results in the ordinary way

Subject	Procedure	Deg.	Diam. (min)	Duration (msec)	Quanta in S_1	r_1/n_1	Quanta in S_2	r_2/n_2	Log $F \pm S_{(\log F)}$	F %
H.B.	1	15	46	86	151	35/53	73	4/47	$\bar{2}{\cdot}75 \pm 0{\cdot}16$	5·6
H.B.	1	15	9	7·8	125	45/55	60	13/45	$\bar{2}{\cdot}66 \pm 0{\cdot}17$	4·6
R.W.	1	15	9	7·8	142	26/45	68	2/28	$\bar{2}{\cdot}72 \pm 0{\cdot}21$	5·2
J.R.	1	15	9	7·8	123	38/57	59	10/51	$\bar{2}{\cdot}56 \pm 0{\cdot}18$	3·6
P.M.	3	15	9	7·8	208	33/40	100	13/61	$\bar{2}{\cdot}59 \pm 0{\cdot}15$	3·9
							Mean	(5)	$\bar{2}{\cdot}66 \pm 0{\cdot}08$	4·58
H.B.	2	6·9	46	86	263	36/46	186	22/54	$\bar{2}{\cdot}58 \pm 0{\cdot}24$	3·8
					302	39/45	166	17/55	$\bar{2}{\cdot}53 \pm 0{\cdot}16$	3·4
					324	37/44	155	11/56	$\bar{2}{\cdot}44 \pm 0{\cdot}14$	2·8
					363	50/52	135	4/48	$\bar{2}{\cdot}66 \pm 0{\cdot}12$	4·6
					427	42/44	123	4/56	$\bar{2}{\cdot}44 \pm 0{\cdot}12$	2·8
							Mean	(5)	$\bar{2}{\cdot}53 \pm 0{\cdot}09$	3·39
A.G.	3	6·9	46	86	363	42/48	174	17/52	$\bar{2}{\cdot}27 \pm 0{\cdot}16$	1·9
					363	41/52	174	9/47	$\bar{2}{\cdot}31 \pm 0{\cdot}15$	2·0
					159	33/53	76	7/49	$\bar{2}{\cdot}50 \pm 0{\cdot}18$	3·2
					240	33/46	115	4/54	$\bar{2}{\cdot}65 \pm 0{\cdot}14$	4·5
					363	46/53	174	6/47	$\bar{2}{\cdot}57 \pm 0{\cdot}12$	3·7
							Mean	(5)	$\bar{2}{\cdot}46 \pm 0{\cdot}17$	2·88

entry are close to the limits for complete temporal and spatial summation, those for the other four being well inside.

The average of these results is 4·6 %. A good many experiments not included in the table have yielded lower figures, and although a reason could not always be found for this, the following factors can cause low results and may have been responsible. The first is faulty setting of the intensities of the flashes: this is considered later, but lower values of F are obtained if the intensities are either too high or too low. A second difficulty is that 'threshold' as determined by the self-setting technique was almost always found to be considerably higher at the end of a run than it was at the beginning, and in some cases there was a drop in the proportion of flashes classified as brighter towards the end of a run. When, as in these experiments, the subject can give himself flashes of known and constant intensity, he is aware of these fluctuations in threshold, and can attempt to compensate, but it is not surprising if he is not wholly successful. Thirdly, subjects sometimes have periods of 'bad-seeing' due to interference by various spurious sensations, or they may lose their criteria as a result of long sequences of stimuli which they have to classify alike.

The highest figure obtained in any experiment in which I had confidence was nearly 8 %: an occasional result as high as this is to be expected if the true figure is 5 %, with sampling error of determinations ± 1·5 %.

The next two sections of the table give lower figures for F because they were done closer to the fovea, but they are included to show (*a*) that the ratio of upper to lower intensity is not an important variable and (*b*) that reproducibly high figures can be obtained in unselected series. The middle section shows all the results obtained by one subject on one day in an experiment in which the ratio of the intensities of the pair of stimuli was varied from 3·5 : 1 to 1·4 : 1. The subject was dark-adapted but the stimulus lay only 6·9° from the fovea. Another minor difference is that the subject gave himself a regular sequence of upper intensity, lower intensity, unknown (Procedure 2), omitting the first ten or twenty counts while he was establishing his criterion. In this case the stimulus area and duration are a little above the limit of complete summation. It will be seen that the ratio of stimulus intensities makes no significant difference to the estimate of F; the less complete separation achieved with the smaller ratios is just what would be expected from the increased difficulty of the task. However, the sampling error increases with the small separation, and it would become inconveniently large if it were reduced further. It is also inconvenient to use too large a ratio, because then there may be no false classifications, and hence the estimate will be incomplete.

The bottom section of the table contains the first five estimates done on a new subject under the same stimulus conditions as the previous lot, but with a fixed ratio of about 2:1. In this case the subject was classifying the unknowns according to whether he saw them or not (Procedure 3) and gave himself no trials of known intensity. The improvement in the series is marginal.

In all these three experiments the standard error of the estimates can be calculated from the 5 experimental determinations in the normal way. This figure is given after the mean, and it can be compared with the calculated sampling error of each individual estimate. In each group the scatter of experimental results is not greater than the calculated sampling errors would lead one to expect, so that there is no indication that the groups are not homogeneous.

The conclusions drawn from these experiments are:

(1) Efficiencies of intensity discrimination close to 5 % can be obtained at 15° in the nasal field.

(2) Efficiency is lower (*ca.* 3 %) at 7° in the nasal field, and is not much affected by the intensity ratio of the pair, which does, however, affect the accuracy of the estimate.

Exposure to known stimuli

In calculating the performance of the ideal device it is assumed that complete knowledge of the intensities, variabilities and other parameters (area, position, duration, and instants of occurrence) of the stimuli is available. One must ensure that these are also available to the subject, and the most direct way of doing this is to allow him to look at will at samples of the pair of stimuli. The results in Table 1 suggest that this is not terribly important in the neighbourhood of threshold, where the occurrence of a sensation provides a ready-made criterion for discriminating between the classes. This conclusion is confirmed by the following experiment, and is extended to the task of discriminating between a pair of stimuli which are both well above threshold.

In all cases the eye was dark-adapted, the 6·9° nasal field was used, and stimuli were 97 min diameter, and 86 msec duration. For the first condition, the pair of stimuli straddled the threshold, and the subject (H.B.) classified simply according to whether he saw the stimuli or not; there were no exposures of stimuli of known class, but the first few unknowns were not signalled. The efficiency obtained was 3·3 % ($\log F = \bar{2}{\cdot}52 \pm 0{\cdot}15$). The subject then repeated the determination with the same intensities of stimuli, but giving an exposure of upper, then lower, before each unknown; he obtained an efficiency of 2·8 % ($\log F = \bar{2}{\cdot}45 \pm 0{\cdot}15$), which is not significantly different. Both stimuli were then increased by a factor of ten, so that they were both easily visible on all trials. The subject saw about ten stimuli of each class, and then sorted an uninterrupted sequence of 123 unknowns, with no indication of which was which other than his visual experience. His efficiency was 0·45 % (log F = $\bar{3}$·66 ± 0·12). He repeated the run with exposure of known stimuli before each unknown, and obtained the marginal improvement to 0·69 % (log F = $\bar{3}$·84 ± 0·15).

There is an obvious decrease in efficiency on increasing the stimuli to suprathreshold levels. It might have been thought that this was because there is no internal criterion to act as a discrimination level once the stimuli are above threshold, but the attempt to restore efficiency to the previous level by repeating the standard stimuli is not successful. It was concluded that, provided the subject has a few trials before the run, he has adequate knowledge of the stimuli he has to discriminate. In fact, in most of the estimates to be given, he has been able to see samples of the standards whenever he wants to, and his knowledge of them has been further increased by signalling whenever he made a false classification, so that the preceding 'unknown' became 'known' as soon as he had classified it.

Effect of stimulus intensity

Figure 1 shows an experiment in which the mean intensity of the stimulus pair was varied, keeping the ratio constant. For the left-hand set of points there was no background, the eye was dark-adapted, and the 46 min diameter 86 msec duration stimulus fell in the 6·9° nasal field. The intensities of the upper and lower members of the pair are given by the right and left borders of the rectangles. The top and bottom represent the mean plus and minus one standard error. The value of the threshold, determined by the usual self-setting technique, is indicated by the arrow over the curve.

It will be seen that F is highest for stimuli which approximately coincide with the threshold in intensity, and it falls off quite rapidly both below and above this intensity. Experiments have not been done to determine whether the coincidence holds under a wide variety of conditions, though preliminary observations suggest that this may be so. It should, however, be pointed out (1) that if the coincidence did not hold it would presumably be possible to obtain higher efficiencies by the discriminative method than could ever be obtained by threshold or frequency-of-seeing curve methods, (2) that the coincidence is not predicted by current theories of threshold; it is apparently a new feature of subjective thresholds that needs accounting for.

The right-hand set of points in Fig. 1 shows how efficiency varies when the eye is adapted to a background which sends $1{\cdot}12 \times 10^6$ quanta sec^{-1} deg^{-2} into the eye. The light from the central 46 min diameter spot of this large adapting field came from a glow modulator tube connected to a switching and timing circuit such that it could be turned to one of a randomly selected pair of intensities either above or below its starting intensity for a period of 87 msec. The subject's task was, as usual, to decide whether an unknown belonged to the brighter or dimmer class, and efficiencies were calculated in the normal way. It will be seen that the determinations lie near a curve which has been displaced down and to the right compared with that holding in dark adaptation. There are three points to note about this curve. First the peak is lower; the optimum efficiency of the light-adapted eye is never as great as that of the dark-adapted eye, as will be shown again in the next section. The second point concerns the position of the peak; the two arrows above the curve show the approximate values of M for the threshold increment and decrement of the stimulus spot. The discrimination between two quantities of light again appears to be optimum when the quantities in the flash are close to the least change that is detectable. Unfortunately the method is not sensitive enough to detect whether there is a decline in efficiency between the threshold for increment and that for decrement of the adapting light. The third point to note in Fig. 1 is that although the peak in the light-adapted eye is lower than in the dark-adapted eye, the curve lies above

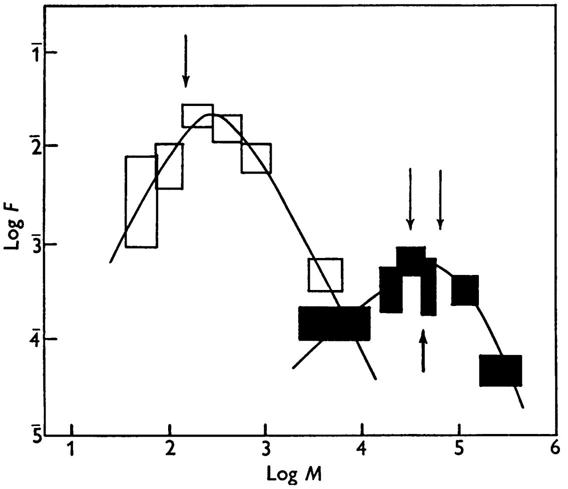

Fig. 1. Log efficiency for discriminating pairs of stimuli of different intensities. M is the average number of quanta entering eye during the stimulus including those from the background over the area of stimulus. Left curve: dark-adapted eye, 6·9° nasal field, stimulus area 0·46 deg^2, duration 0·086 sec. Right curve: eye adapted to uniform field of intensity $1 \cdot 12 \times 10^6$ quanta sec^{-1} deg^{-2}, stimulus position, area, and duration as above. Stimulus spot could be momentarily decreased or increased in intensity. Edges of rectangles represent upper and lower intensities, and mean value of log F plus and minus one standard error. Arrows above curves show thresholds, and that below shows the value of M for zero deviation from the adapting intensity.

the (extrapolated) curve for the dark-adapted eye. In other words, light-adaptation improves the discrimination of bright flashes, but never to the extent that the efficiency rivals that of the completely dark-adapted eye. (The significance of the arrow below the curve will be referred to in connexion with Fig. 3.)

This improvement was confirmed in several experiments where flashes were added to a uniform background as in the usual method for investigating increment thresholds. For instance, with the eye dark-adapted the logarithm of the efficiency of discriminating between two stimuli 10 and 20 times threshold was $\bar{3}{\cdot}88 \pm 0{\cdot}14$. The eye was then adapted to a background where $\log I = 4{\cdot}19$ (I measured in quanta $\text{sec}^{-1}\,\text{deg}^{-2}$), and the logarithm of the efficiency for the same pair of stimuli, now added to the background, improved to $\bar{2}{\cdot}46 \pm 0{\cdot}13$. Adaptation to this background improved the eye's efficiency at discriminating the stimuli almost 4 times. In the same experiment the log-efficiency of the dark-adapted eye at discriminating two flashes 330 and 165 times threshold was $\bar{4}{\cdot}26 \pm 0{\cdot}20$; on adapting to a background of $\log I = 6{\cdot}12$, the log efficiency improved to $\bar{3}{\cdot}83 \pm 0{\cdot}12$, an efficiency almost 40 times better than the dark-adapted performance.

The improvement also occurs if the stimuli, instead of being superimposed upon the background, appear in a small unilluminated patch in it. Fig. 2 shows determinations with varying intensities of flash done in this way at three background intensities. Although the adapting field surrounding the stimulus zone undoubtedly shifts the curve in the same direction as a complete adapting field, it does not move so far; the arrows under the curves represent the number of quanta expected from the background in the area and duration of the stimulus, which are the same as in Fig. 1. It will be seen that in this case the peak is well short of the arrow, whereas in Fig. 1 it was almost over it. However, in spite of this, the optimum efficiency is still obtained when the intensities are near threshold. In interpreting this experiment one must remember that the region upon which the stimuli fall has been illuminated at the full intensity of the background in the recent past because of eye movements, and is illuminated by scattered light from the background at the time when the stimuli actually arrive.

A potentially misleading feature of the method of plotting results used in Figs. 1 and 2 (and also Fig. 3) should be mentioned at this point. To illustrate this, suppose that a subject adopted an unusually low criterion for classifying stimuli as brighter: the consequence would be that almost all the brighter stimuli would be correctly dealt with, but that many of the dimmer would be incorrectly classed. Now if the decline in efficiency with increasing intensity is associated with the change in criterion that usually follows when the intensity of the stimuli that are to be discriminated is raised, then a subject who followed the above tactic when the intensities were raised might maintain a higher efficiency at the higher intensity. In point of fact no subjects did this: the numbers of false responses of the two kinds were roughly equal so that, in very nearly every case, the discriminant level (Barlow, 1962, p. 162) lay between the two stimulus intensities. A simple method of avoiding this difficulty would be to plot as abscissa the discriminant level rather than the intensities of the stimuli used.

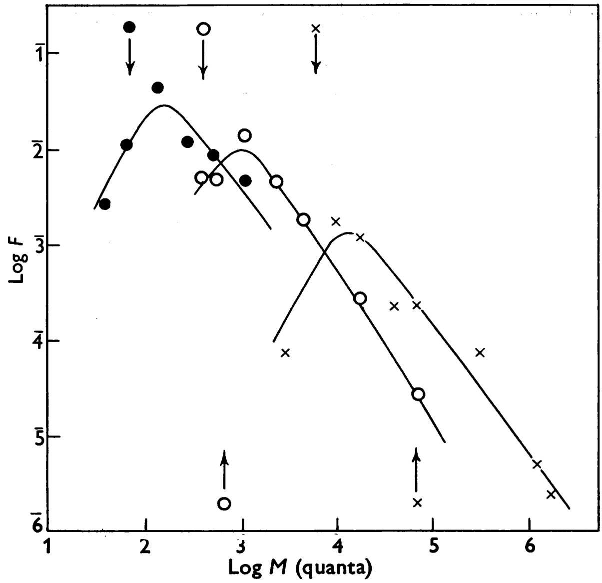

Fig. 2. Log efficiency when the stimulus fills a dark window in an otherwise uniform adapting field. Area of window and stimulus 0·46 deg^2 (46 min diam.); duration of stimulus 0·086 sec. Arrows above curves show the threshold for a stimulus appearing in the window. Arrows below show the value of M if the stimulus equals the background in intensity. Left curve: zero background. Middle curve: log (background intensity) = 4·5 (intensity measured in quanta sec^{-1} deg^{-2}). Right curve: log (background intensity) = 6·5.

The exploratory experiments reported in this section are not a detailed survey of the effect of all the variables considered, but they point to the following tentative generalizations.

(1) Highest efficiencies are obtained when the pair of stimuli to be discriminated are both in the neighbourhood of the subjective sensory threshold.

(2) The optimum for the light-adapted eye is lower than the optimum for the dark-adapted eye.

(3) Light adaptation increases the quantities of light which are optimally discriminated, and for these larger quantities the efficiency is higher than for the unadapted eye.

The effect of light adaptation

The object of the experiment shown in Fig. 3 was to determine the optimum efficiency of the rod system when discriminating between two stimuli superimposed upon a uniform adapting field. The field was in this case orange, the spectral composition being that resulting from light of the illuminant (colour temperature approx. 2750° K passing through an Ilford 204 filter; this transmits virtually everything of wave-length longer than 600 mμ, and virtually nothing shorter than 580 mμ). Following Aguilar & Stiles (1954), this was chosen in order to light-adapt and thus desensitize the cones more than the rods, in this way allowing the behaviour of the rods to be followed up to higher levels.

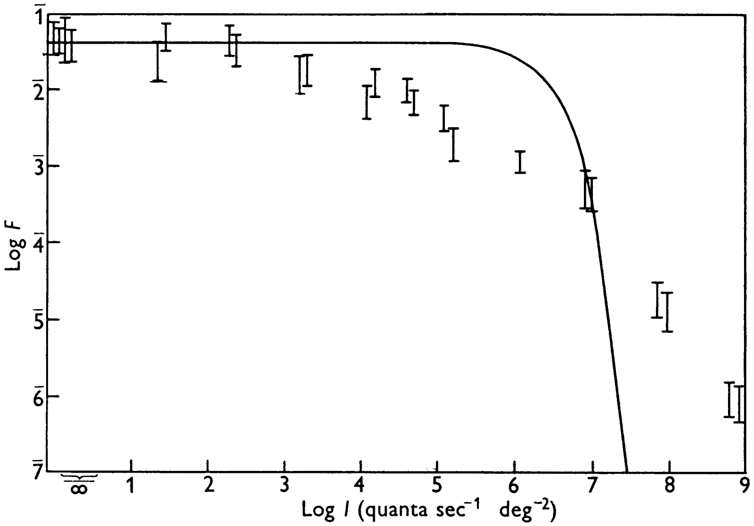

Fig. 3. Log efficiency for varying background intensity I. Stimulus area (0·46 deg^2; 46 min diam.) and duration (0·086 sec) were chosen to yield optimum efficiency (see text). They were added to a uniform background of log intensity shown on abscissa. Bars show mean log$F$ plus and minus one calculated sampling error. Pairs close together were done at the same background. Line shows prediction of compartment hypothesis (see Discussion).

If one wishes to determine the minimum quantity of light required for threshold, then in choosing stimulus conditions one simply has to ensure that both area and duration are below the figure at which complete areal and temporal summation break down. The same choice will not yield optimum quantum efficiency, and instead of choosing conditions to minimize $\Delta I . AT$, one must choose them to minimize $\Delta I . (AT)^{\frac{1}{2}}$. The reason for this involves two stages of argument. First, the ideal detector must sample over areas and times equal to the area and duration of the expected stimulus, for if they were more the noise would be unnecessarily high, and if they were less the signal would be unnecessarily small. Where stimulus and sampling area and duration coincide, the signal–noise ratio is $\Delta I . AT/(I . AT)^{\frac{1}{2}}$. The second stage of the argument is that where this signal–noise ratio is lowest, the most stringent demands are being put upon the ideal device and the required quantum efficiency is highest. With I constant, this is where $\Delta I . (AT)^{\frac{1}{2}}$ is least, and on a plot of log ΔI against log A (or log T), it is just beyond the limit of complete summation, at the point where the curve is tangent to a line of slope $-\frac{1}{2}$. This optimum is not a sharp one, because Piper's Law ($\Delta I \propto A^{\frac{1}{2}}$), and the corresponding square-root law for time, are roughly true for a range just beyond the limits of complete spatial and temporal summation. Thus, in spite of the fact that these limits vary with adaptation level, it is possible to choose a fixed value for area (46 min diam.) and time (86 msec) which, on the basis of the threshold data previously published (Barlow, 1958*a*), yield the optimum figure for F at all backgrounds.

The results of the previous section show that the intensity of the pair of increments to be discriminated is important, and that the optimum is obtained for increments close to the threshold determined by the self-setting technique. Although this has not been shown to hold for all conditions, it does appear to be true for stimuli of the area and duration used here when superimposed on a uniform background, and when the eye is adapted to that background. Accordingly, in the present series of determinations, the threshold was first determined several times, the average was taken, and the pair of flashes were chosen to lie one above, and one below this intensity.

Figure 3 shows that, in spite of these precautions to ensure that the performance was near optimum at each background, there is clearly a decline as the adapting intensity is increased. This decline starts at about $\log I = 2{\cdot}5$ (I measured in quanta $\sec^{-1}$ $\deg^{-2}$), and has a slope of about $-\frac{1}{2}$ on this plot, implying that $F \propto I^{-\frac{1}{2}}$. This continues up to $\log I = 7$. At this background log F is about $\bar{4}{\cdot}60$ (0·04 %), roughly 1/100 of its value in complete dark adaptation. Thereafter the efficiency declines more rapidly to very low values. This series of observations has been repeated on another subject with similar results.

The rapid decline at high intensities occurs at a level well below that at which saturation occurs. Aguilar & Stiles (1954) define the saturation level as the background intensity which causes the Fechner fraction ($\Delta I/I$) to increase to 100 times its plateau value, and in all their four subjects it was close to log $I = 3{\cdot}7$ (I in scotopic trolands), i.e. log $I = 9{\cdot}35$ (I in quanta sec^{-1} deg^{-2}). The point at which the Fechner fraction started to increase was rather less than a tenth of this, 8·15 log quanta sec^{-1} deg^{-2} (2·5 log scotopic trolands). This is at the extreme upper end of the range studied here.

The conclusions drawn from this experiment are that efficiency decreases with light-adaptation even when stimulus area, duration, and intensity are optimal, the decrease being as shown in Fig. 3. The question whether other conditions could be found in which higher values of F could be obtained in light-adaptation will be discussed later, and at the same time the reason why these experiments do not show a decrease in efficiency at low intensities, where Rose (1948) and Clark Jones (1957) did find a decrease, will be pointed out.

DISCUSSION

There are three matters requiring discussion: first, the possibility that improved methods would yield higher figures for quantum efficiency, either in dark-adaptation, or after light-adaptation; secondly, the mechanisms which may be responsible for the loss of efficiency that have been described; thirdly, the significance of the conditions which yield optimum efficiencies.

Are higher quantum efficiencies attainable?

The aim of the investigations described is to throw light upon the mechanisms of the retina and visual pathways by finding out how efficient they are, and the conditions under which their efficiency declines. We shall get the clearest information where the efficiency is highest, for there are many possible inefficient mechanisms, but comparatively few types of efficient ones. Rose (1948) made this point by describing the gap between the ideal and the actual performance of the eye as the 'logical space' within which physiologists could legitimately postulate hypothetical mechanisms. The first point to discuss, then, is whether the experimental observations have yielded the highest possible efficiencies, for if they have not we have failed to exclude mechanisms that might have been excluded.

Consider first the measurements on the dark-adapted eye. Anything which causes performance to vary, other than the actual quantum fluctuations themselves, will cause efficiency to drop. For instance, carelessness on the part of the subject, such as might result from discomfort or boredom, would do so, but I doubt if this is an important factor in the results shown in Table 1. Hecht, Shlaer & Pirenne's frequency-of-seeing curves took much longer to obtain, and lapses on the part of the subject might be expected to be more important, yet their efficiencies are if anything higher. Training may have a small influence, but the authors of this and the above paper must be considered as fully trained, and the average of their efficiencies is only just above that of the inexperienced subjects of Table 1. Fluctuations in accommodation were eliminated with homatropine in one very careful trial; the result was no higher than usual. With a very small test stimulus, eye movements might cause fluctuations in the fraction of the light which falls on non-rod elements (cones, blood vessels) in the retina, and thereby decrease efficiency. Bouman & van der Velden (1947) did in fact observe a steepening of the frequency-of-seeing curve when the area of stimulus increased, and this might be associated with an increase of efficiency. Sufficient tests have not been done to exclude this, but in complete dark adaptation the improvement in efficiency on increasing the area of the stimulus is marginal, if it occurs at all: the increase with area which occurs in the light-adapted eye is of course a different matter.

The present work indicates a figure close to 5 % for the highest quantum efficiency of the human eye, but there are some published results that suggest a higher figure. The early claims of Rose (1948) and Clark Jones (1957) must be discounted for reasons they have themselves given. Those of their calculations that yield high figures have introduced unjustifiable restrictions into the performance of the ideal detector with which the eye is compared, and specific criticisms have been made in the previous paper (Barlow, 1962).

Values for F can, however, be derived from Hecht *et al.* (1942) and from Baumgardt (1960) that are distinctly higher than 5 %. These are obtained by dividing the value of c for the best fitting cumulative Poisson curve by the number of quanta entering the eye for 55 % seeing. For the five experiments that Hecht *et al.* tabulate in full the mean is 6·0 %, the estimated standard deviation of the determinations being $\pm$ 1·4 %. Baumgardt's four subjects give $7{\cdot}3 \pm 1{\cdot}5$ %. The difference between these and my figure of $4{\cdot}6 \pm 0{\cdot}85$ % is in both cases statistically significant ($P < 0{\cdot}01$). It might be thought that the difficulty of performing absolute light measurements at low intensities was the cause of this discrepancy, but this explanation is not borne out by inspection of our actual values for the absolute threshold. For Hecht *et al.* the average 55 % threshold for the five tabulated results is 112 quanta; for Baumgardt's four subjects it is 101 quanta; the average discriminant level (see Barlow, 1962, p. 162) for the top five results of Table 1 is 117 quanta. The main cause of the discrepancy turns out to lie in the slope of the response function. Expressed as the average value of the apparent criterion c, this is 6·6 for Hecht *et al.*, 7·25 for Baumgardt, and 5·4 for my results. Baumgardt presented his stimuli in blocks all of the same intensity; although he mixed blanks with the stimuli, there might still have been some 'channelling' of responses and consequent steepening of the response curves. On the other hand there are two features of my experiments that might have caused flattening, namely, the relatively inexperienced subjects employed, and the more rapid rate of presenting stimuli. Another factor that should probably be borne in mind in a re-examination of the problem is the possibility that a minor degree of dark-adaptation can continue to occur for a very long time (Achmatov, 1927).

Because of these discrepancies, the only certain conclusion at the moment is that the highest quantum efficiency of human vision lies in the range 4 to 8 %; but it may well turn out that the best subjects under the best conditions yield figures very close to that here derived from the result of Hecht *et al.*, namely, 6·0 %.

The other important figure to discuss is the efficiency achieved in discriminating increments superimposed upon an adapting field, for we should like to know the mechanisms causing the loss of efficiency during light-adaptation. Figure 3 shows an efficiency of 0·04 % at an adaptation level of 10^6 quanta sec^{-1} deg^{-2}: is it possible to achieve higher efficiencies in the light-adapted eye?

The answer is certainly 'yes' if one is using cones under conditions nearly optimal for them, for the calculations of Barlow (1958*b*) and Clark Jones (1959) suggest a figure of about 0·5 %. But we are here interested in the loss which occurs in the rod system when it is light-adapted. The parameters optimized in the test of Fig. 3 were the area and duration of the increments, and their intensities relative to the threshold. There is here a small gap, unlikely to be important, in that area and duration were chosen from threshold data, not measures of efficiency. Another more important possibility is that the rectangular pulses of light with sharp well-focused edges may be badly matched to the temporal and spatial weighting functions used in the integrating mechanisms of the retina. Suppose, for instance, that because of its weighting functions the retina has to pick up from the background twice as many quanta as those which fall within the area and time of the stimulus. The noise it has to contend with will be $\sqrt{2}$ times what we suppose, and the efficiency we calculate will be reduced to $\frac{1}{2}$. Now in fact we have to account for a reduction to 1/100, and it is hardly plausible to account for all of this by a simple mismatch of this sort.

Is it possible that the retina is organized to perform some other task more efficiently than the one we are setting it? The retina and visual centres might, for instance, detect movement, or linear contours, more efficiently than small patches of light at a higher intensity than the background. It would certainly be interesting to compare performance at these tasks, but it is hard to believe they will turn out to be 100 times as efficient as intensity discrimination.

Causes of reduced efficiency

The overall efficiencies which have been measured can be broken down into stages as follows: (i) transmission through the optic media, (ii) absorption in the rods, (iii) activation of rods, (iv) detection of activity by later stages in the nervous system. Efficiencies are multiplicative and it is a merit of this method of expressing results that one can so simply allow for known losses in transmission and absorption, thus showing the residue of inefficiency which must be accounted for by other mechanisms. Rushton (1956*b*) estimates that 10% of light incident at the cornea is absorbed by rhodopsin in the rods. Accepting this, the efficiency of the first two stages is also 10%. Taking 5% as the overall efficiency, this means that the efficiency of activation and detection is 50%. Two explanations are offered for this remaining inefficiency. (1) Rods are activated by a product of bleaching, or the act of bleaching, but not by the initial activation of a rhodopsin molecule by an absorbed quantum. Wald & Brown (1953) found the efficiency of bleaching to be near 60% *in vitro*, and Hagins (1955) found the same in the intact rabbit retina. Rushton's (1956*a*, *b*) data also support the assumption that it is near 60% *in vivo*. (2) Rods are excited by every absorbed quantum, but they also discharge spontaneously, possibly as a result of thermal activation of rhodopsin. It has been shown (Barlow, 1956) that this idea is compatible with the data on the absolute threshold, and we here require the intrinsic noise to reduce efficiency by 50%.

The present results do not allow one to rule out either of these possibilities, and they may both apply, as the following calculations show. From the first cause alone the calculated overall efficiency would be 6%. From the second alone it would be 7·2%, using a figure of 400 quanta $\text{sec}^{-1}\ \text{deg}^{-2}$ for the dark light based upon determinations of the increment threshold done on one of the subjects during the course of the present experiments. From both together it would be 4·3%. All these figures are just compatible with the estimates reported here, though 7·2% is rather high and accordingly dark light is unlikely to be the sole cause of lost efficiency. It should probably also be pointed out that Rushton's figure of 10% for the fraction of entering light that is absorbed in rods, used in the above calculations, is only a best estimate. His evidence excludes a lower figure more convincingly than it excludes a higher figure.

One further point about intrinsic noise is worth noticing. Both Rose (1948) and Clark Jones (1957) reported a drop in efficiency at low adaptation levels which could be attributed to it, but no such drop appears in Fig. 3. The reason for this is that the stimulus intensities were here chosen to be optimum, and they were consequently raised beyond the range susceptible to the dark light. Where they are reduced below the optimum, as in Figs. 1 and 2, a decline does occur that might be caused by dark light, but one cannot proceed far along these lines without an explanation for the decline that occurs above the optimum.

Loss of efficiency in light adaptation

It is certain that this loss is not caused by changes in the amount of light absorbed in the receptors, for the adapting intensity required to reduce significantly the concentration of rhodopsin is many times higher than the highest adapting intensity used here. Hence the loss must be caused by changes in the efficiency of rod activation, or in the efficiency of detection of changes in the number of rods activated. As an example of a mechanism causing the former type of loss in light adaptation the hypothesis of refractory compartments proposed by Wald (1954) will be considered. As an example of something causing the latter type of loss, we shall consider briefly the 'scaling hypothesis', which postulates that the loss of information occurs when many quantal absorptions have to be signalled by a small number of nerve impulses. It is important to remember that other hypotheses could be advanced, for the eye here functions inefficiently, and inefficiency can be caused in countless ways.

Refractory compartments

There are three attractive features of this hypothesis. First, it postulates that bleaching of one molecule of pigment inactivates a whole compartment containing many molecules, and thus it explains why light-adaptation causes much greater loss of sensitivity than could be explained by the simple bleaching of pigment. Secondly, the only compartments remaining excitable when a certain adapting light has been applied are those that have absorbed zero quanta; this is the first term of the Poisson series which tells one the probability of x events occurring if the average number is a;

$$P(x|a) = \mathrm{e}^{-a}(a^x/x!)$$

and for zero events this is simply e^{-a}. Now if a proportion P of the compartments remain excitable, it is reasonable to assume that the threshold will be increased by a factor $1/P$, which in this case is e^{a}. Hence the hypothesis predicts that log threshold increase shall be proportional to the amount of pigment bleached, and this is what Rushton (1961) has found to be the case experimentally. The third attractive feature is that it is very easy to postulate a mechanism whereby the inactivation of a compartment is linked to the concentration of rhodopsin, rather than to the number of molecules bleached in the recent past, thus explaining the persistent loss of sensitivity after exposure to a light. This can either be done by supposing that the compartment remains refractory until the bleached molecule is regenerated, as Wald assumed; or one could assume that the refractory period is much shorter, but that the compartment is also insensitive for a similar period during and immediately after regeneration of a molecule.

The curve in Fig. 3 shows the prediction of the compartment hypothesis as proposed by Wald. The important constants are the number of rhodopsin molecules per compartment, here taken as 12,900; the average regeneration time, here taken as 520 sec; the probability of a given rhodopsin molecule being bleached per quantum per square degree entering the eye, here taken as $7{\cdot}02 \times 10^{-14}$; and the fraction of quanta entering the eye that activate the rods, here taken as 5 % to make the curve fit the low-intensity efficiency measurements. It is clear that there is no quantitative fit, and the fact that efficiencies at high intensities are higher than predicted rules out the hypothesis in this form. The whole theoretical curve can be shifted to the right by assuming a smaller compartment size; the measured efficiencies would then all lie below the predicted values, and additional losses could be postulated to account for the difference. But it is clear enough that the hypothesis of refractory compartments does not, by itself, explain the loss of efficiency we are concerned with here.

'Scaling' loss

An alternative explanation which attributes loss of efficiency to 'scaling' will be briefly outlined. The ideal device always deals with the actual number of quanta absorbed within a certain area and duration. These numbers are very large at high intensities; for instance, for the highest background intensity in Fig. 3 about $2{\cdot}5 \times 10^6$ quanta are absorbed within the area and duration of the stimulus, and at the saturation level defined by Aguilar & Stiles (1954) more than 10,000 quanta/sec are being absorbed by each rod. It is not reasonable to assume that every quantum absorbed is signalled to the discriminating mechanisms: what, then, will be the effect upon efficiency if the number of nerve impulses is less than the number of quanta absorbed? The answer will, of course, depend upon the exact way in which the reduction is brought about; signalling only a randomly selected fraction would reduce the efficiency by this fraction, and binary coding would enable the number of impulses to be reduced to $\log_2$ (number of quanta) without any loss.

A more detailed treatment of this problem will be developed elsewhere. Briefly, it is assumed that the significant effect of a change in the number of quanta absorbed over a particular area and time is to cause a change in the number (rather than the timing) of impulses from that area. The number of extra quanta required to produce an extra impulse is called the 'scaling factor', and it reduces the information available centrally about the number of quanta absorbed. Making the plausible assumption that the scaling factor increases with adaptation level, it is possible to account for the loss of efficiency in light-adaptation. Furthermore, lateral inhibition would be expected to increase the scaling factor for large stimulus areas more than for small stimulus areas; hence light-adaptation, which increases the amount of lateral inhibition, should cause a greater loss of efficiency for large test areas than for small, as is found to be the case.

The significance of optima

It has been shown in this paper that the quantum efficiency for the discrimination of intensity varies when the test conditions vary, and is at its best for particular test conditions. This applies to the intensity of the stimuli being discriminated: they must be near the threshold for the particular conditions considered. It applies to the adaptation level, which must be as low as possible to achieve the highest efficiencies. On the other hand, if the intensities of the stimuli to be discriminated are fixed at a high level, it will in general be best to adapt the eye to an intensity at which these stimuli are near the threshold. Clark Jones (1957, 1959) has shown that it applies to the area and duration of the stimuli, and this is to be expected from the well known relations between area and duration and threshold.

It is fairly easy to account for the existence of optima, for they would occur in any practical detector. What is not so easy to account for is the fact that they are often much broader than the simple model would lead one to expect. For small stimuli, quantum efficiency declines rather slowly with increasing adaptation level; and the efficiency declines less rapidly with areas or durations greater than the optimum than one would predict if the eye had integrating units with fixed parameters. It is these broad optima which make the eye such a versatile instrument, and it should be remembered that only one of the four parallel photochemical systems has been considered in this paper. It is a challenge to determine the mechanisms which endow the eye with this versatility. Rose was impressed by it, and suggested that the retina must have some mechanism akin to the automatic gain control of a radio. The suggested 'scaling factor', dependent upon adaptation level and area of stimulus, is an attempt to put this hypothesis in a form that can be tested quantitatively both in psychophysical experiments and in discharges recorded from single units in the optic pathways.

The fact that the efficiency of discriminating between stimuli that lie well above the dark-adapted threshold can be improved by light-adapting the eye is a confirmation of Craik's (1938, 1939) view that light-adaptation is more than a simple loss of sensitivity. He anticipated Rose's analogy of an automatic gain control by comparing light-adaptation to changing the range-setting switch of a multi-range meter. This improvement of discrimination at high intensities also fits in with the ideas proposed by Keidel, Keidel & Wigand (1961).

In addition to their implications about the mechanisms involved, the existence and positions of these various optima throw an interesting light upon what might be called the 'design' of the visual system. Innumerable tasks have to be performed under widely varying conditions, and the visual system could hardly be so laid out that all these tasks were performed up to the limits determined by the numbers of quanta absorbed in the retinal receptors. As in most engineering situations, the design adopted must be a compromise, and in these measures of efficiency we see where high performance is maintained and where sacrifices are made. Presumably this reflects the decrees of natural selection as to which tasks are important, which less important.

SUMMARY

1. The overall quantum efficiency of vision has been determined from the ability to discriminate between two lights differing from each other in intensity.

2. The highest efficiencies found were nearly 5 %, and they were obtained in the following conditions: near-threshold intensities of light of small to moderate area and duration in 15° nasal field of the dark-adapted eye.

3. Efficiency is reduced when the lights to be discriminated are (*a*) below or (*b*) above the subjective sensory threshold.

4. The highest attainable efficiency is reduced by light-adaptation.

5. Light-adaptation increases the intensities at which discriminative efficiency is optimal. Because the decline in 3(*b*) above is steeper than that in 4, light-adaptation improves the efficiency of discrimination of bright lights.

6. The optimal efficiency is discussed in relation to intrinsic noise and the efficiency of excitation of rods by absorbed quanta.

7. The loss of efficiency in light-adaptation does not conform to the predictions of the 'compartment hypothesis', but might be caused by the increase of the 'scaling factor' that relates the number of extra quanta absorbed to the number of extra signals sent centrally.

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