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Chapter 16

THE PHYSICAL LIMITS OF VISUAL DISCRIMINATION

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1. Introduction

The eye, with its associated nervous structures, is the sense organ used to extract information about the environment from the light that reaches an animal. This is a physical description of its function, and the two purposes of this chapter are to describe physical factors that limit the performance of this task, and to discuss various anatomical and physiological features of the eye in relation to these limits.

To say the eye extracts information from light is of course a very incomplete description, for it omits to mention that the information extracted is specifically related to particular biological functions. For instance, the nestling gull extracts the information that the beak in front of it has a red dot on it, and it responds to this by gaping for food. The specificity of stimulus and response prompts the question: Is it any use just paying attention to the physical process? Are there not always specific aspects of a visual discrimination that are really more interesting than the very general process "extracting information"?

The biological aspects certainly are important and interesting, but they are far too complex to handle theoretically. On the other hand, we can in certain cases calculate theoretical physical limits for the extraction of information, given the task being performed, the environmental situation, and the relevant anatomical and physiological features of the eye. One thus has the possibility of making an interesting comparison for one can see how nearly the biological performance approaches the best possible performance. This is one of the few opportunities one has of assessing biological performance on an absolute scale, and I hope the reader will be convinced by the end of this chapter that this comparison improves one's understanding of much that is already known about the eye. But there is another aspect that is more important.

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The biological performance is necessarily worse than the best possible performance, and by taking into account more and more of the eye's characteristics we may account for much of the discrepancy. What remains to be accounted for remains to be discovered, and thus our attention is drawn to points about which we are ignorant. This is even more valuable when one sees how the eye's performance changes when the physical conditions change. Sometimes the change parallels that of a physical model. But sometimes it does not, and here again our attention is focused upon something we do not understand. Thus the main benefit of the present approach is to reveal the important, performance-limiting features of the eye—both those we do know about, and those we do not.

1.1 Extracting Information from Light

The process of extracting information may conveniently be divided into three stages. First, the light is split up. Second, the amounts in each part are measured—that is, signals are generated which vary in some way according to those amounts of light. Third, decisions are made based upon the collection and comparison of signals from different parts of the image.

The splitting up can be exemplified by the action of a camera lens, or a spectroscope, or a photocell and recording oscilloscope. The lens forms an image in which the intensity of light over separate small regions corresponds to the intensity of light striking the lens at particular angles. In the spectroscope lights of different wavelengths pass to different points in the plane of the spectrum where they can be separated from each other, and the record of the photocell output allows one to separate out the amounts of light falling at different instants of time.

Now the eye splits up the light in all these three ways simultaneously. Its lens forms an image on the retina, which extracts information as to color as well as intensity, and signals back to the brain continuously. It may be added that bees can detect the plane of polarization of light, and its degree of polarization (von Frisch, 1950), which necessitates even further splitting up in that case. However, there are no other physical properties of the light which would provide a basis for splitting it up: the direction of entry, spectral distribution, the time of entry, and polarization properties, exhausts the list of primary possibilities. There are, however, secondary properties (e.g., phase relations of light entering at different angles) that, as far as is known, are not utilized.

Physical examples of what is meant by "measuring" are the production in photography of a variable number of silver bromide crystals changed in such a way that they can subsequently be developed, or the liberation of electrons from a photocathode and causation of a variable deflection in a galvanometer. In the eye the nature of the graded signals

passing from the receptor cells to the ganglion cells is unknown, but from ganglion cells to the brain one is dealing with familiar all-or-none nerve impulses.

In physical instruments the final decisions are usually left to the operator, who identifies features in the photograph, lines in the spectrum, or characteristically shaped deflections in an oscilloscope. These are operations one is tempted to put on one side as "psychological," and too complex to consider at present from a physical point of view. But there are indications that the process of collecting, comparing, and deciding starts in the retina: since these operations tend to lose information they cannot be entirely neglected if we want to explore the limits of extraction of information from light, even at an elementary level.

1.2 Importance of Measuring

It might seem natural to consider the three stages in the order in which they occur—splitting, measuring, and deciding—but there are reasons for regarding the second stage as the most basic. Unlike the simple camera, spectroscope, and photocell, which each do only one operation, the eye does all three at once: because it has to signal time of entry, it cannot integrate light over long times, as can the photographic plate; because it has to signal direction, it cannot integrate in space; and because it has to signal color, it cannot integrate over the whole spectrum. At a later stage, of course, these integrations may be performed, but the information will by then have been decreased by any losses caused when the quantities in the separable parts were measured and signalled. The consequence, then, of the thorough splitting up of the light is that the quantities in each of the subdivisions are very small, and if these quantities are too small to be measured satisfactorily, the splitting will have been fruitless. Conversely, the better the measurements that are possible, the finer the splitting up that will be worthwhile. To put it another way, the accurate measurement of quantities of light is one of the keys to high acuity, good color discrimination, and high speed of response. Because it occupies this key position, it is considered first, and more space is devoted to it.

Four sections of this chapter are concerned with measuring light. Section 2 deals with the well-known and well-established effects of quantum fluctuations at the absolute threshold of vision. In Section 3 the effects of quantum fluctuations under nonthreshold conditions are considered, and in Section 4 the hypothesis of intrinsic noise as a limiting factor is introduced. There follows in Section 5 a discussion of the influence of various instrumental features of the eye—its size, shape, etc.—on the physical limit to performance set by quantal fluctuations and intrinsic noise.

Of the remaining four sections, two (Sections 6 and 7) are devoted to

splitting up the light, one to the problem of making visually based decisions, and the final one summarizes the chapter as a whole.

2. Quantum Fluctuations at Threshold

2.1 Theory

Light is absorbed and emitted in quanta, rather than continuously. The size of these units of energy is given by the product of Planck's constant h , which has the dimensions $m^2 t^{-1}$, and the frequency, ν , of the light emitted or absorbed. For a light of wavelength $510 \text{ m}\mu$:

$$h\nu = 3.9 \times 10^{-12} \text{ ergs}$$

This is the ultimate limit to the sensitivity of any light detector, and it will be shown later that visual receptor cells approach this limit closely. There is, however, another aspect of the size of the quantum which is perhaps more basic than this. It determines how accurately a given quantity of light can be measured. Quantal absorptions are random, independent events, which means that only probabilities can be accurately specified before the events happen. If many events are expected, the uncertainties with regard to each one balance out and deviations from the expected number are relatively small, but if only a few events are expected, relatively big departures from expectation occur. It is the same with our individual expectations of life and the insurance companies' expectation of profit. The energy per quantum determines how many quanta there are in a given amount of light, and hence it is this energy that also determines how accurately the amount can be measured.

To illustrate the statistics of this process we shall consider the behavior of an idealized photocell. In Fig. 1 a source of monochromatic light illuminates a photosensitive cathode through a shutter. The shutter opens to admit a brief pulse of light and a certain number of quanta strike the photocathode. Some of these quanta cause an electron to be emitted; let us suppose that our arrangements are so perfect that every emitted electron is detected and counted, and that electrons are only emitted as a consequence of light falling on the photocathode. Now if the shutter is repeatedly opened while the physical conditions are kept constant, the number of photoelectrons emitted on each trial can be counted and these numbers will be found to be distributed approximately as shown in Fig. 2.

The distribution is that described by Poisson:

$$P(n|s) = \frac{s^n e^{-s}}{n!}$$

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$P(n|s)$ = probability of n events occurring if the average number is s . A textbook of statistics should be consulted for the theoretical derivation of this formula. The condition for it to be applicable is that the events that occur are only a small selection from a very large number m of

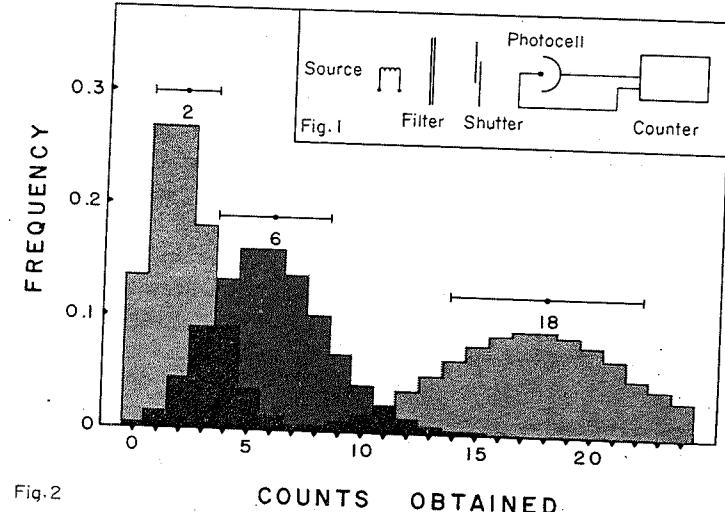


Fig. 2

COUNTS OBTAINED

FIG. 1. Arrangement for counting quanta. The physical conditions only determine the *average* count obtained: individual exposures will yield numbers different from the average count, and these will be distributed approximately as shown in Fig. 2.

FIG. 2. Three overlapping Poisson distributions showing (ordinates) the expected frequency of occurrence of counts of 0, 1, 2, 3, ... (abscissa) when the average number is 2 (left histogram), 6 (middle), and 18 (right). Lines over the histograms are of length $2\sqrt{\text{average}}$. Left and middle distributions overlap more than middle and right, although their averages differ by the same factor.

possible events, each of which has a very low probability p of occurring: $s = pm$, but p is small and m is large. If this were not the case, the distribution would be different, and indeed one might have to take this into account when considering lights so bright that a large proportion of the available molecules absorb a quantum. But one need not worry about this for ordinary lights.

Notice that the distribution depends solely upon s , the average number of events. It does not matter in the least what combination of distance, exposure, or any other factor, finally leads to the occurrence of this average number of electron emissions: for all combinations, this number completely specifies the distribution.

Since this is so, the scatter of the distribution must also be uniquely related to s , and in fact the relation is exceedingly simple. The standard

deviation (square root of variance) of the distribution is equal to the square root of its mean. Thus the scatter of the distribution (\sqrt{s}) increases as s increases, but the relative scatter ($\sqrt{s}/s = 1/\sqrt{s}$) becomes smaller as s increases.

Though tables are available (Molina, 1942), the Poisson distribution is rather inconvenient to handle, and various approximations are often made. The one most frequently used is a normal distribution with the same mean and standard deviation as the Poisson to be approximated. This is symmetrical and continuous, instead of asymmetrical and discontinuous, and it is not a good approximation if the average number of events is small (say less than 20). However the fact that most people are familiar with the normal distribution, and the standard deviation as a measure of its scatter, makes it useful in introducing the concepts involved; furthermore the errors of the approximation are usually small by biological standards. It will therefore be used in much of this article, but two better ones are worth mentioning. The first is a normal distribution of $\log n$, the second a normal distribution of \sqrt{n} . The latter has the added feature that the standard deviation is constant—distributions like those of Fig. 2 plotted with \sqrt{n} as abscissa do not get broader as n increases.

This introduction has shown: first, that there is a minimum amount of light, 1 quantum, and that it is physically impossible to detect quantities smaller than this; second, that the absorption of greater quantities is inevitably subject to variability; and third, that the variability is relatively less (though greater absolutely) when the quantity of light is greater.

2.2 Experiments of Hecht, Shlaer, and Pirenne

In 1942 Hecht *et al.*, published a very thorough investigation of the minimum quantity of light that can be detected. The following is a brief résumé of their work; others at about the same time or subsequently have contributed to this problem, and they will be referred to in Section 2.3.

Having reviewed previous measurements of the threshold, Hecht *et al.* determined in pilot experiments the conditions that led to the lowest values. These were: thorough dark adaptation; the use of monochromatic light of wavelength $510 \text{ m}\mu$; the use of peripheral retina 20° from the fovea; a small area of test stimulus (a disk 10 min in diameter); brief duration of test flash (1 msec); and attending to the comfort and convenience of the subject.

These investigators then made careful physical measurements of the intensity required for a stimulus to be seen in 60% of trials. Seven reliable subjects (i.e. subjects who very rarely, if ever, responded to a "blank")

gave figures for this threshold energy, measured at the pupil of the eye, ranging between $2.1 \times 10^{-10} \text{ erg}$ and $5.7 \times 10^{-10} \text{ erg}$. Converted to quanta, these are 54 to 148 quanta.

The next step was to find out what became of these quanta. Hecht and his co-workers estimated that not more than 10% were absorbed in the receptor cells so that only 5 to 14 quanta are on average absorbed when the weakest possible sensation of light is experienced. There were at the time several uncertainties in arriving at the figure of 10%, but subsequent work (see Rushton, 1956b) has tended to confirm it.

Five to 14 quanta absorbed is already a low figure for the threshold, but this is the total number absorbed from the stimulus. Some 300 rods are covered by the geometric image of the stimulus, and the light must actually be distributed over a larger number. The probability that one of these rods absorbs 2 or more quanta can be calculated, and for the conditions of the experiment described above it turns out to be a little lower than the probability of seeing the stimulus flash. Hence Hecht *et al.* argued that, although about 10 quanta are absorbed from a threshold stimulus, it is not necessary for any rod to absorb more than a single quantum in order that the stimulus should be seen. In other words, receptors must be excitable by the absorption of a single quantum.

One can criticize this stage of the argument if it is based on the results of Hecht *et al.*, because the calculated probability is only a little below the experimentally determined one. However, if one repeats the calculation using threshold measurements made with larger stimulus areas, when the conditions are less favorable for 2 quanta being absorbed in a single rod, the margin is much greater. Their conclusion is certainly right.

Apparently then, receptors reach the ultimate in sensitivity, and can respond to the absorption of a single quantum of radiation. But do they always so respond, or is it possible that they only occasionally respond? If the receptors only responded on about one trial in ten, that might explain why some ten rods must each absorb a quantum before the threshold is reached. This possibility is not excluded by their measurements of threshold energy, but it is excluded by their experiments on the sharpness or abruptness of the threshold. Before considering the argument let us look at the evidence.

The experiment is to determine the frequency with which a subject sees stimuli of various intensities near the threshold level. If the threshold was absolutely abrupt, then one would see none of the stimuli of lower intensity, but all those of higher intensity. In point of fact the intensity has to be roughly doubled if it is to be seen on 95% of trials, and roughly halved if it is to be invisible on 95% of trials. Figure 3 shows the experimental determinations on Hecht, Shlaer, and Pirenne themselves.

The classical interpretation, from Fechner on, of the lack of precision of threshold is in terms of "biological variability." Threshold was supposed to change from moment to moment, so that the same physical stimulus was sometimes below it, sometimes above it. But quantum fluctuations of the type shown in Fig. 2 provide an alternative explanation: if

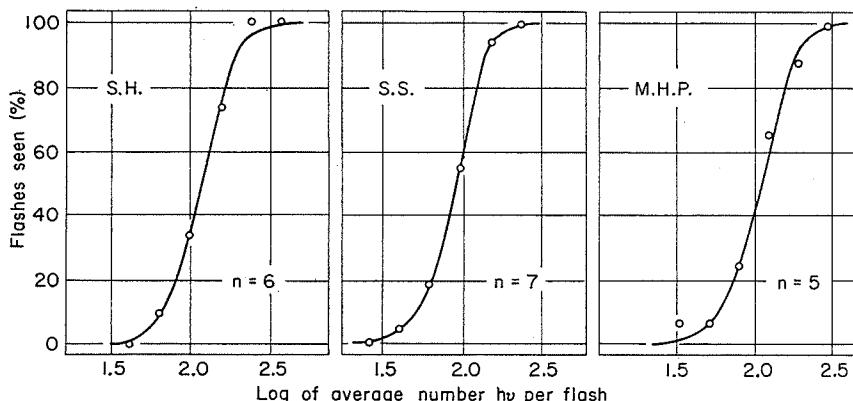


FIG. 3. Relation between the average number of quanta in a stimulus flash and the frequency with which it is seen by three observers. Each point represents 50 stimuli, except for S.H. where it is 35. These were presented in a random sequence. Curves are cumulative Poisson curves as shown in Fig. 4: 6, 7, and 5 are therefore lower limits to the number of quanta required for seeing the flash. (From Hecht *et al.*, 1942.)

physical conditions are absolutely constant, the number of quanta absorbed will vary, and this number may sometimes be below, sometimes above, a stable unvarying biological threshold. To decide which explanation is correct one must calculate how much variability is caused by the quantum fluctuations, and compare it with the actual variability. This is what Hecht *et al.* did.

Figure 4 shows theoretical frequency-of-seeing curves calculated on the following basis. For the curve marked $n = 1$, one calculates (or looks up in tables) the probability that one or more events occur if the average number is that whose logarithm is plotted as abscissa. A frequency-of-seeing curve, plotted with log intensity as abscissa, would be of this same shape if threshold depended upon the occurrence of a single critical event. For instance, the hypothesis that rods have only a $1/10$ chance of signaling a quantal absorption and that one such signal suffices for threshold, would lead to this curve. It would not of course be in this position because a large fraction of the entering quanta are lost, but this fraction will be the same for each intensity, and will be represented by the same distance

on the logarithmic scale. Hence by sliding this curve along the abscissa we should get it to fit the experimental points.

A glance back at Fig. 3 will show that the curve would not fit at all. The experimental values run from near 5% to near 95% over only 0.6 log units, whereas the curve for $n = 1$ requires almost 2 log units change: the

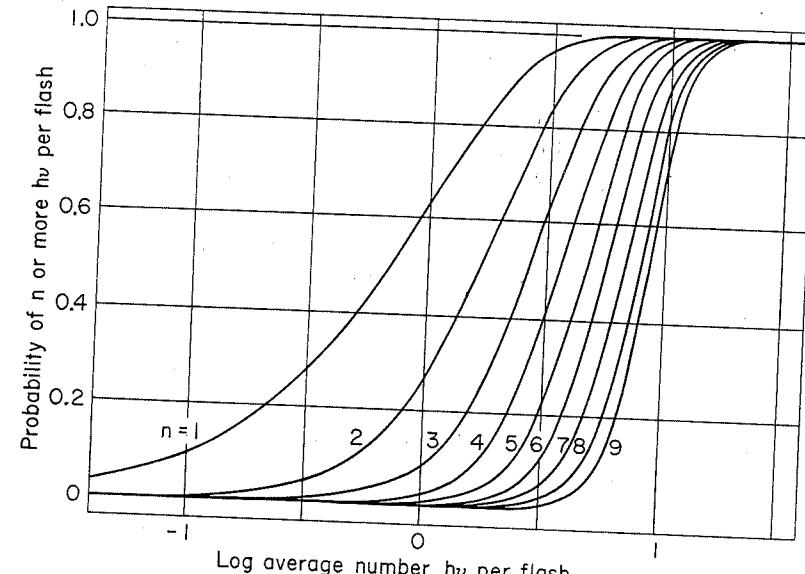


FIG. 4. Cumulative Poisson probability distributions. Ordinates give the probability that n or more quanta will be absorbed when the average number absorbed is whose log is given as abscissa. A frequency-of-seeing curve when n quanta are required for threshold cannot be steeper than the cumulative Poisson for that value of n . (From Hecht *et al.*, 1942.)

human visual system is more stable—it has a much less variable threshold—than the hypothesis led us to expect. Notice that the disagreement is in a direction which enables one to say definitely that the hypothesis is wrong. If a certain random variability of response is introduced at an early stage in the visual process, then no subsequent operations can eliminate it. Hence when the variability is found to be *less* than predicted, the hypothesis is convincingly disproved. Had we found a discrepancy in the other direction, we could only have said that there were other sources of variation in addition to that implied by the hypothesis—a much weaker statement.

At this point a cautionary comment must be made. Frequency-of-seeing curves are sometimes determined in such a way that the variability of response is underestimated. The most usual method is to repeat each

intensity many times consecutively: except for the first member of such a series of stimuli, the subject has experience of the preceding stimuli and can utilize this in forming a judgment about whether a light was present. Clearly when he is exposed to a stimulus the subject should judge entirely by the effects of that particular stimulus on his visual system, and should not take into account ancillary information. The only way to ensure that he behaves like this is to make certain that no ancillary information is presented, i.e., the stimuli must be presented in random order. In this way spurious steepening of the experimental curves can be prevented.

Now returning to Fig. 4, it will be seen that the curves get progressively steeper for higher values of n . Which one fits the experimental data best? In Fig. 3, curves for $n = 6, 7$, and 5 are drawn, and are seen to provide a satisfactory fit. The conclusion is that the threshold required at least $6, 7$, or 5 rod signals in these cases: had it required less, the relative variability would have been greater than that observed.

Hecht *et al.* estimated that 5–14 quanta were absorbed from a threshold flash of light, and they took this calculation from the frequency-of-seeing curve as a confirmation of their direct estimate, adding that it proved that biological variation of threshold was not the major cause of the uncertainty range at threshold. This conclusion remains valid, but it should be pointed out that the results do *not* show that there is no variation whatever caused by events inside the visual system: they only show that the physical source of variability, quantum fluctuations, are important. It may also be mentioned that their conclusion leaves us with a question in our minds: Why, if a rod can respond to a single quantum, do we need about ten rod activations in order to see? Intrinsic noise causing a danger of false responses is a possibility: the quantitative consequences of this idea have been worked out (Barlow, 1956, 1957a) and are discussed further in Section 4.

2.3 Other Work on Threshold

At about the same time as Hecht *et al.* were doing the work described above other investigators were getting interested in quantum effects in vision. Van der Velden (1944) concluded that only 2 quanta were required at threshold, and this has received some support in subsequent work (Bouman and Van der Velden, 1947; Baumgardt, 1953). The evidence for a 2, as against 5–8, quanta-threshold is twofold. First, frequency-of-seeing curves were obtained fitting $n = 2$. This method gives a lower limit to the number of quanta required, since additional sources of variability will flatten and not steepen the curves. For this reason more weight is bound to be attached to properly conducted experiments that

yield steeper curves, and opinion has swung in favor of the higher value of threshold. A second argument for a 2-quantum threshold was based upon the form of curves relating the threshold to the area and duration of the stimulus light. Here again there are alternative explanations for the square root relations predicted on the 2-quantum hypothesis and found experimentally. However, for a recent review of the arguments and experiments favoring the 2-quantum hypothesis, see Bouman (1961).

Baumgardt (1953) has suggested a modification of the 2-quantum hypothesis that reconciles some of these differences, and has recently (1960) made another careful physical measurement of the absolute threshold which agrees well with Hecht *et al.* The reader is referred to reviews by Pirenne (1956, 1962) and to Brindley's book (1960) for further discussion of this and other work on quantum fluctuations at the absolute threshold.

2.4 Conclusions

It is clear from the work described that the physical limit to performance set by the quantal nature of light is important first because receptors sometimes reach this limit, and second because quantal fluctuations account for a large part of the apparent variability of the absolute threshold.

It is natural to ask if quantum fluctuations are important when the eye is performing tasks other than detecting the weakest possible lights. Before discussing this, the inaccuracy of measurement caused by quantum fluctuations will be explained.

3. Limits to Measurement above Threshold

3.1 Theoretical Aspects

In Sections 2.1 and 2.2 we showed how random fluctuations in the numbers of quanta absorbed caused there to be a range over which the probability of seeing a stimulus increases gradually rather than in a sudden step. These fluctuations clearly limit the accuracy with which quantities of light can be measured, for identical physical stimuli lead to variable results. Thus a glance at Fig. 2 shows that a single trial at an intensity which causes an average of six emissions will often yield as little as one-half or as much as two times the average value.

The effect of quantal fluctuations can be expressed another way. Suppose that in a series of stimuli made under constant conditions causing an average of six emissions we interpolate some trials made with a higher intensity causing an average of 18 emissions. The distribution of numbers of electrons emitted for the higher intensity is as shown for the right-

hand distribution, and it can be seen that the number of events is usually different from that for the left-hand distribution; if the apparatus is set to indicate when, say, 11 or more events occur, then on average only 3.7% mistakes would be made (if equal numbers are presented) and the system would indicate which stimulus had been delivered with moderate efficiency. But now consider the case where stimuli causing an average of six emissions are interpolated among stimuli causing an average of two. The ratio of intensities is the same, but the distributions overlap more and the number of mistakes in discriminating between the stimuli would rise from 3.7% to 14.7%. The reason for this deterioration is that the relative size of the fluctuations has increased as the average number s decreased. Over each distribution is drawn a line of length $2\sqrt{s}$ centered at s ; it will be seen that the left and middle nearly overlap whereas the middle and right are clearly separate. Mistakes are bound to occur when the two average numbers differ by only a few times \sqrt{s} . If s is the average number of events caused by a particular light, then the smallest increase in that light that can be detected is $\Delta s = K\sqrt{s}$, where K is a factor determining the minimum number of mistakes that can be made, and is of the order 1 to 5.

If we now define F as the fraction of quanta entering the eye that cause rod excitation, N as the average number of quanta entering from the light, and ΔN as the weakest increment in N that can be detected, we can write

$$\Delta s = F \Delta N = K\sqrt{s} = K\sqrt{FN}$$

$$\Delta N = K\sqrt{N}/\sqrt{F}$$

For a given reliability, the smallest increment that can be detected is lower the higher the proportion of incident quanta that are utilized. It is thus theoretically advantageous to catch more quanta, not only at absolute threshold, but also in order to improve discrimination at higher intensities.

Consider the case where the eye is detecting a test stimulus of area A exposed for a time T at an intensity ΔI , which is being added to a uniform background of intensity I . Then substituting ΔIAT and IAT for ΔN and N yields

$$\Delta I = K\sqrt{I}/\sqrt{ATF} \quad (1)$$

Imagine fixed values for ΔI , I , and K : now if A is progressively reduced there will come a point where ΔI is below the physical limit, and the test stimulus cannot be detected. However, it will be observed that the value of A at which this occurs is inversely related to F , and hence

the larger F , the smaller the areas within which small differences of intensity can be detected. Catching more quanta has theoretical advantages for improving acuity as well as for lowering the differential and absolute thresholds, and it is clear from a similar argument that it is also potentially advantageous for temporal resolution.

3.2 Experiments at Levels above the Absolute Threshold

These are the theoretical considerations, but is there any evidence that quantum fluctuations limit performance except at threshold levels of illumination, where we already know that they are important? First notice that the temporal and spatial resolving power of the eye improves as the general level of illumination increases. These changes in performance were reviewed by Hecht (1937) and interpreted in terms of the kinetics of bleaching and resynthesis of photochemical pigments. De Vries (1943) and Baumgardt (1947) pointed out that the photosensitivity of the pigments would have to be inordinately high for this interpretation to be correct, and together with Rose (1948) and Mueller (1950) they drew attention to the possibility of interpreting these changes in terms of quantum fluctuations. The suggestion was that as luminance increases, the quantities of light in progressively smaller temporal and spatial subdivisions reach a level where quantum fluctuations no longer hinder the discrimination of intensity differences. It is hardly possible to doubt that the decreased relative size of the quantum fluctuations is one factor allowing improved resolution at high luminances, but it is now clear that it is not the only factor, except perhaps in special circumstances.

This is most clearly shown in studies of the increment threshold, where the theoretical, quantum-fluctuation-limited performance can be calculated with fewer arbitrary assumptions than is the case with most tests of spatial and temporal resolution. Figure 5, from Aguilar and Stiles (1954) shows log (increment threshold) plotted against log (background field) under conditions such that rods alone were operative over the whole range. The curved line represents the average experimental result on four subjects, and the straight line is calculated on the assumption that 5% of the light entering the eye is absorbed in the rods. It is clear that both theoretical and experimental thresholds rise with increasing background intensity, and that the experimental thresholds are always higher than the theoretical limit. But the limit is nowhere very close to the experimental curve.

Barlow (1958a) did experiments in which the area and the duration of the test stimulus were varied as well as the background intensity. As was well-known, ranges of test conditions were found for which ΔI was proportional to $T^{-1/2}$, $A^{-1/2}$, and $I^{1/2}$, and this might be taken to support

the idea that quantum fluctuations limit performance. However Eq. (1) says that it will hold for all of them, and no test conditions were found where this was true. If A and T were small, ΔI was proportional to $I^{1/2}$, but not to $A^{-1/2}$ or $T^{-1/2}$, and for other test conditions one of the other

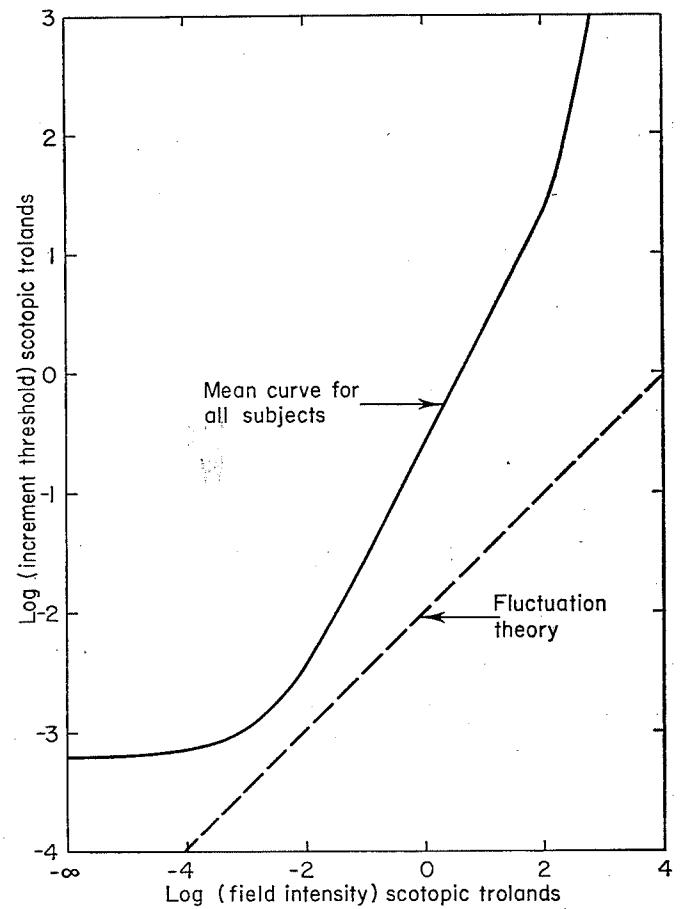


FIG. 5. Relation between log (increment threshold) and log (background field intensity) under conditions chosen so that rods alone determine threshold. The incremental stimulus is of large area, and duration 0.2 sec (cf. Fig. 6). Dotted line shows lowest attainable increment threshold if 5% of quanta entering the eye are utilized, and if K of Eq. (1) is 5. (From Aguilar and Stiles, 1954.)

predictions of Eq. (1) broke down. Thus one must clearly reject the idea that quantum fluctuations are the only factor limiting threshold, and the only factor that changes when the light entering the eye increases.

However one cannot for this reason neglect them altogether. They are

certainly present, and what has to be explained is not the shape of the experimental curve as plotted, but the gap between the experimental curve and the theoretical line.

3.3 Quantum Efficiency

At this point the concept of Quantum Efficiency will be briefly mentioned. This was introduced by Rose (1948) and followed up by Clark Jones (1959) and Barlow (1958b, 1962a,b). The concept is most simply defined as the ratio

$$\frac{\text{Minimum possible number of quanta required for performing a task}}{\text{Number actually required for the task}}$$

Where the gap between the experimental and theoretical lines in Fig. 5 is small, the eye is doing almost as well as it can on the 5% of incident quanta that were assumed to be absorbed in the rods: hence on the above definition the quantum efficiency almost reaches 5%. But where the gap is big, the eye is performing at a level which could theoretically be reached if a far smaller percentage of the quanta were absorbed, and hence the quantum efficiency is far below 5%. Quantum efficiency is thus a useful measure of performance, for it takes quantum fluctuations into account and shows up when and where other factors are causing performance to change. It has other advantages in enabling comparisons to be made where they would otherwise be impossible, and these are discussed elsewhere (Barlow, 1962a).

3.4 Causes of Efficiency Loss

The bends in the experimental line of Fig. 5 suggest that there are four factors causing a loss of quantum efficiency:

1. There are one or more factors that prevent performance from reaching the theoretical limit even at the most favorable background intensity of about 1/1000 troland (td). This may be partly due to the fact that the stimulus area and duration used by Aguilar and Stiles were not chosen to give the optimum performance. The effects of a mismatch between the stimulus and the neural mechanisms for collecting together information from groups of receptors are discussed further in Section 8.2.

2. The second factor causes an increasing loss of performance relative to the theoretical limit as the background intensity falls below 1/1000 td. This is plausibly accounted for by a random process causing "noise" in the receptors, and this will be considered in Sections 4.1-4.9.

3. A third factor causes a progressively increasing loss as the luminance level increases above 1/1000 td. This is the inescapable conclusion whenever the Weber law ($\Delta I \propto I$) holds, but Fig. 6 (Barlow, 1957a) shows

that this factor does not always play a part. The line here is the theoretical one derived from fluctuation theory, and it will be seen that the experimental points fit it well. (The line levels off at low backgrounds because background noise has been introduced into the theory—see Sections 4.2 and 4.3.)

In Fig. 6 quantum fluctuations satisfactorily account for the rise of ΔI with I , whereas in Fig. 5 they do not. The experiment was similar to that of Aguilar and Stiles, the eye operating in the scotopic range, and the increment being added to a uniform adapting field. The difference lay

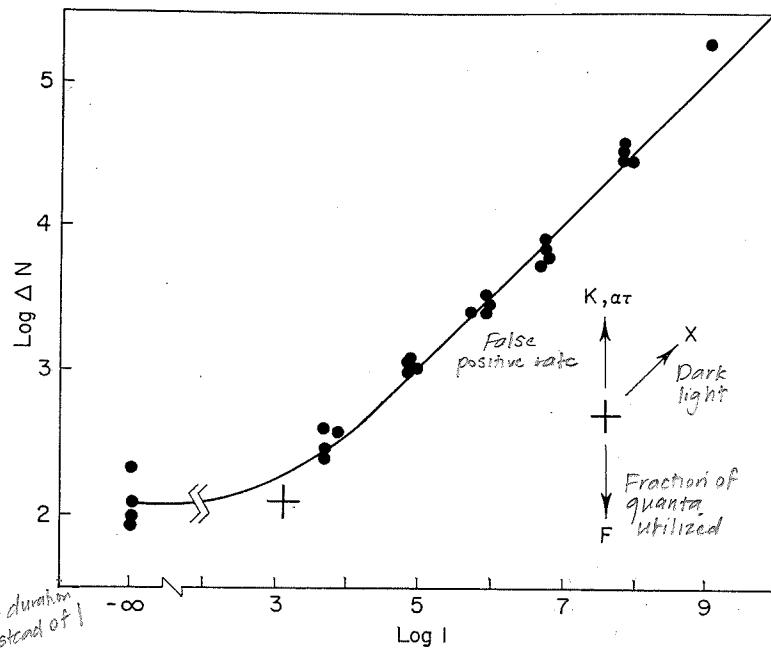


Fig. 6. Relation between log (increment threshold) and log (background intensity) under scotopic conditions. The experimental points lie on a line of slope $1/2$ rather than 1 as in Fig. 5 because the incremental stimulus is small (diameter 7.1 min) and brief (8.6 msec). The curve is $\Delta N = K(I + X)^{1/2}$. $\alpha^{1/2}\tau^{1/2}/F^{1/2}$ (see Sections 4.2 and 4.3), and the arrows at bottom right show how the curve is shifted by increases in the different quantities. (From Barlow, 1957a.)

in the type of stimulus used; in Fig. 6 it was of small area and duration, whereas in Fig. 5 it was large and lasted 0.2 sec. With brief, small stimuli the square root law $\Delta I \propto I^{1/2}$ replaces the familiar Weber-Fechner law, $\Delta I \propto I$, and conditions can be found where foveal cones yield similar results (Barlow, 1958b).

When the amount of light entering the eye increases, the relative mag-

nitude of the quantum fluctuations decreases. Apparently the visual system is so designed that it can exploit this change when detecting small, short-duration stimuli, but cannot exploit it when detecting large, long-duration stimuli. We can see that it is advantageous to favor signals from small areas that last for short times, for the spatial and temporal resolution of the system is thereby improved. Furthermore, one can guess that lateral inhibition is the variable factor that causes the change, for it increases in light adaptation (Barlow *et al.*, 1957). However we cannot translate this suspicion into quantitative predictions about overall performance, mainly because we do not know what causes the progressive loss of efficiency with light adaptation when using large stimuli. The Weber-Fechner law is so deeply entrenched in our thinking that we tend to accept it as "natural," but it is not: it implies a loss of efficiency increasing in proportion to \sqrt{I} , and it is time we knew what causes this loss.

4. At the top of Fig. 5 the experimental curve rises almost vertically, which was attributed to "saturation" of the rods by Aguilar and Stiles (1954). Fuortes *et al.* (1961) worked on a rod monochromat, and showed that saturation could not be explained by cones "grabbing" the nerve pathways, or any other such interaction. In a subsequent paper Rushton (1961b) showed that saturation intensity is nearly independent of the eye's adaptation level. Its cause is intriguing and remains unknown, but it should be pointed out that it is quite difficult to choose conditions under which it is clearly shown. Under natural conditions it cannot often be a factor that prevents the eye from making a discrimination.

3.5 Conclusions

This discussion of the experimental evidence on quantum fluctuations at nonthreshold levels has brought out four factors (Section 3.4) that prevent the visual system from performing up to the theoretical limit. Two of these, noise and the effects of mismatch, are discussed in following sections. Mechanisms for the others are unknown, but contrasting the actual performance with the physical limit at least forces us to recognize our ignorance.

4. Noise as a Limit to Light Measurement

4.1 General Discussion

To reduce the effect of quantal fluctuations we have seen that it is necessary to catch and count as many as possible of the quanta that are available. The detector must, then, be sensitive, and sensitive devices have a tendency to respond spontaneously. In a physical device, it is the

number of these spontaneous responses that determines the intrinsic noise level, and this is the factor limiting the ultimate sensitivity. For instance in a photocell electrons leave the photocathode even in complete darkness causing the "dark current." This is not simply like a zero error, for the stream of electrons fluctuates and introduces random errors over and above those due to quantal fluctuations. Furthermore it is the fluctuating dark current, rather than the fluctuating quantal absorptions, that limits performance at low luminance levels.

From this analogy with a photocell we get the idea that "sensitivity" is not simple. To specify performance we need to know two quantities, the ratio of electric current to incident light, and the value of the dark current, i.e., the current that flows in total darkness. The first of these limits performance under most conditions, but it is the second that determines the lowest luminance levels at which the cell will operate satisfactorily.

The reasons for introducing the idea of an intrinsic noise, analogous to dark current, can be summarized as follows. First, it is *a priori* likely in view of the eye's sensitivity. Second, even the most reliable subjects give occasional "seen" responses to zero stimuli; and these must have some physical origin. Third, the optic nerve shows an irregular discharge of impulses even in complete darkness (Kuffler *et al.*, 1957; Bornschein, 1958). Fourth, one is subjectively aware of visual sensations even in complete darkness. There are thus ample grounds for introducing the idea, but of course the important questions are whether intrinsic noise can be measured, and whether it is useful in describing quantitatively the performance of the eye and changes in this performance. It turns out that the answers are in the affirmative. Indeed much confusion in the past has resulted from considering sensitivity as a simple property. This will emerge in the discussion of two topics, the comparison between rods and cones, and the changes that occur in dark adaptation. First the effects of noise will be described in greater detail.

4.2 Theoretical Effects of Intrinsic Noise

This discussion outlines that given at greater length elsewhere (Barlow, 1956, 1957a, 1958b).

First consider the effect of dark current on the photocell shown in Fig. 1. Suppose that the current is such as to cause an average of x electrons to leave the photocathode during the period the shutter is opened. These spontaneous electron emissions will be random independent events like the emissions caused by light, and will contribute an amount x to the variance. As a result the total variance of the number of electrons passing when an average number s are caused by light will be $s + x$. The normal

approximation to this will have standard deviation $\sqrt{s+x}$, and it is clear therefore that the variability of response is determined by s when $s \gg x$, and by x when $s \ll x$. In other words, dark current is unimportant in determining variability when the light is strong, but becomes the main factor when the light is below a certain level. If Δs , the minimum detectable increment in s , is considered, one sees that

$$\Delta s = K \sqrt{s+x}$$

If, as before, this is written in terms of the intensity, area, and duration of the lights, one gets:

$$\Delta I = K(I + X)^{1/2} / A^{1/2} T^{1/2} F^{1/2} \quad (2)$$

where $FX = x$, or X is the light which causes a photocurrent equal to the dark current.

We thus need two quantities to specify the performance of a photocell. The new one X may be called the "dark light," for it is the light which, when shone into the photocell, causes by its quantum fluctuations an amount of noise equal to the intrinsic noise. The other quantity, F , may be called "quantum-utilizing power," for it is the fraction of available quanta that are utilized. Notice that it is not quite the same as quantum efficiency as defined in Section 3.3, for in obtaining the efficiency no allowance for intrinsic noise is made.

4.3 Experimental Estimates of "Dark Light"

In Fig. 6 the curve has the form of Eq. (2) plotted on logarithmic coordinates, but in determining its position other factors enter the picture. The incremental stimulus was small and of short duration, hence it was the quantity $\Delta I \cdot A \cdot T$ that was important. Equation (2) gives the theoretical limit to detection of such an increment, but we know that the eye summates quanta from the background over an area and duration greater than that of the stimulus. Under these conditions the appropriate equation for the limit is

$$\Delta I \cdot A \cdot T = \Delta N = K(I + X)^{1/2} \alpha^{1/2} \tau^{1/2} / F^{1/2}$$

where α and τ are the area and time over which quanta absorbed from the background cannot be distinguished from quanta absorbed from the stimulus. The effects of mismatch between α , τ , and A , T , are considered further in Section 8.2.

The arrows at the bottom right of Fig. 6 are now nearly self-explanatory. They show how the whole theoretical curve would be shifted by increases in the various parameters. Increasing F , the fraction of quanta utilized, increases the sensitivity for all conditions equally. Increasing

K (decreasing the false positive rate) necessitates an increase in all thresholds, and the same is true if α and τ are increased above the optimum where they are equal to A and T , or if they are decreased below this optimum. However changes in the dark light X have effects distinguishable from these, for they alone shift the curve laterally as well as vertically. Hence it is possible to determine X from the experimental points. Estimates of rod "dark light" from this and other published work have been given elsewhere (Barlow, 1957a), and turn out to be compatible with other data and to resolve some anomalies (Barlow, 1956).

The idea of intrinsic noise has been applied first to the increment threshold obtained with a small, brief stimulus, because the rising limb in Fig. 6 behaves as if it was quantum-fluctuation limited. It is then plausible to postulate an intrinsic source of noise whose variance adds simply to that of the quantum fluctuations. To extend the idea to results such as those of Fig. 5 appears at first sight questionable, for the threshold along the rising limb of this curve is not limited by quantum fluctuation alone. However in Section 3.4 it was shown that, whatever the additional factor may be, it is something whose magnitude increases with light intensity. If we suppose that intrinsic noise has its origin in the receptors, then it may reasonably be expected to have an effect adding to that of real light in causing the threshold to exceed the quantum fluctuation limit. For small stimuli, $\Delta I \propto (I + X)^{1/2}$: arguing along these lines we expect for large stimuli $\Delta I \propto (I + X)$, where X has the same value in the two cases. Experimentally this was found to be the case (Barlow, 1957a).

Notice that the feature of the formulation which leads to this result is the introduction of intrinsic noise at the level of the receptors, where its effects are assumed to add to the effects of light. Many other formulations would be possible; that the present one fits the results favors hypotheses which place the origin of noise peripherally in the visual pathway.

4.4 Descriptive Importance of "Dark Light"

We have introduced "dark light" theoretically, as the manifestation of intrinsic noise in the visual system. However it might have been introduced empirically, as a variable useful in describing differences and changes in visual performance. It would then be defined operationally, as the intensity of background light that just affects the threshold of a superimposed light stimulus. In Figs. 5 and 6 it is the background intensity at the first upward turn of the experimental curve. More exactly, its value is X if it is found that $\Delta I \propto (I + X)^\tau$, where τ lies between 0.5 and 1, depending upon stimulus conditions.

Possibly we are being overhasty in identifying the dark light defined

operationally with intrinsic noise postulated theoretically. But whatever the origin of dark light it turns out to be a very useful concept in comparing scotopic and photopic vision, and in describing adequately the changes that occur during dark adaptation.

4.5 Scotopic and Photopic Vision

Most measures of visual performance show a fairly clear-cut break into two sections. At light intensities of moonlight levels and below, acuity is poor, critical fusion frequency low, colors are not seen, and the peripheral parts of the human retina function more effectively than the central, foveal region. At daylight levels, colors are seen, acuity increases more rapidly with illumination, so does the critical fusion frequency, and the fovea functions more effectively than the periphery (for review, see Pirenne, 1948, or Hecht, 1937). This duality of vision is attributed to the existence of two classes of receptors, rods being the type functioning at low levels, cones at high levels. The same two classes of receptors are found in all vertebrates, and which class is predominant is related to the nocturnal or diurnal habit of the species considered (see Walls, 1942).

It is usually supposed that the duality of function can be attributed to a simple difference of sensitivity of the two types of receptor and their pathways, but from the preceding discussion it is clear that sensitivity must be more accurately defined: Does it mean "quantum-utilizing power" or "intrinsic noise level"?

The threshold number of quanta required by cones can be found by confining light to the fovea, where there are no rods, and adjusting conditions until the lowest threshold is found. According to Arden and Weale (1954) the threshold measured with a small, brief stimulus of white light is as low as it is for rods. The results reviewed by Pirenne (1962) agree that it is low, though not as low as 100 quanta—a figure of 1,000 quanta would perhaps be closer. The estimates of quantum efficiency by Clark Jones (1959) and Barlow (1958b) yield optimum figures of the order 0.5%, as compared to 5% for rods (Barlow, 1962b). Thus the quantum-utilizing power of rods is higher, but only by a factor of approximately 10. In contrast with this quite modest difference, the "dark lights" of the rods and cones have been estimated from Stiles's data, and turn out to be about 10^3 and 3×10^6 quanta (λ maximum)/sec deg 2 : the cones are 3,000 times noisier than the rods (Barlow, 1958b). The difference between scotopic and photopic systems is apparently caused to a small extent by differences in quantum-catching power, but the greater "dark light" of the photopic, cone system is a much more important factor in preventing them contributing at low luminances. A possible physical reason for cones having more intrinsic noise than rods will be considered later.

cone threshold
just as low as
rods

4.6 Dark Adaptation

If the eye is exposed to a very bright light, sufficient to bleach a large fraction of its photosensitive pigments, and then remains in darkness while measurements are made of the smallest quantities of light that can be detected, one obtains the characteristic "dark-adaptation curve." As usually plotted this shows the log of the threshold declining through about 2 \log_{10} units in a few minutes to a plateau where it remains until about 12 min have elapsed: this is the phase of cone adaptation. At about 12 min the threshold starts dropping again to reach its final level, about 3 \log_{10} units lower, after about 30 min. It can be shown that rods alone determine threshold during this phase. Here we can ask the same question about the change in sensitivity of a single system that we previously asked in comparing the two systems, rods and cones: Is the 1,000-fold increase in sensitivity of the rods due to an increase in quantum-utilizing power, or to a decline in intrinsic noise?

Again, the evidence indicates that it is noise that is important. Early evidence came from Crawford's experiments (1937, 1947) in which he compared dark adaptation when measuring the true threshold, as described above, and when measuring the increment threshold when the stimulus was superimposed upon a constant background field of intensity I . If it was quantum-utilizing power that changed, consideration of Eq. (2) (Section 4.2) shows that the two thresholds should have remained separate by a constant factor, $(I + X)^{1/2}/X^{1/2}$, at all times. But if it was dark light that changed, then the increment threshold should have been nearly as low as the true threshold at first, when X was large compared with I , but as X declined to a value low compared to I further changes in its value would make little difference and the increment threshold curve should level off. Crawford (1947) and Rushton (1961b) both found that the latter was what happened, as shown in Fig. 7. Crawford drew the conclusion that the process of dark adaptation could be conveniently described in terms of an "equivalent background light" that declined with time, and he showed furthermore that this transformation completely accounted for the puzzling difference between dark adaptation curves obtained with small, brief stimuli and large ones of long duration. The increment threshold curves for these stimuli are different (Figs. 5 and 6), hence the "equivalent background" affects them differently, and by just the right amount to account for their different dark-adaptation curves. If light adaptation was caused by a decrease in quantum-utilizing power it could be imitated by placing a neutral filter in front of the eye, as suggested by Rushton (1961b): but a neutral filter would affect large and small test stimuli equally, whereas light adaptation affects them

unequally. Hence the best account of the increase of sensitivity that occurs during dark adaptation is in terms of a declining equivalent background light, dark light, or intrinsic noise level.

Dowling (1960) and Rushton (1961a,b) have shown that dark adaptation is also related to rhodopsin concentration, and that log threshold

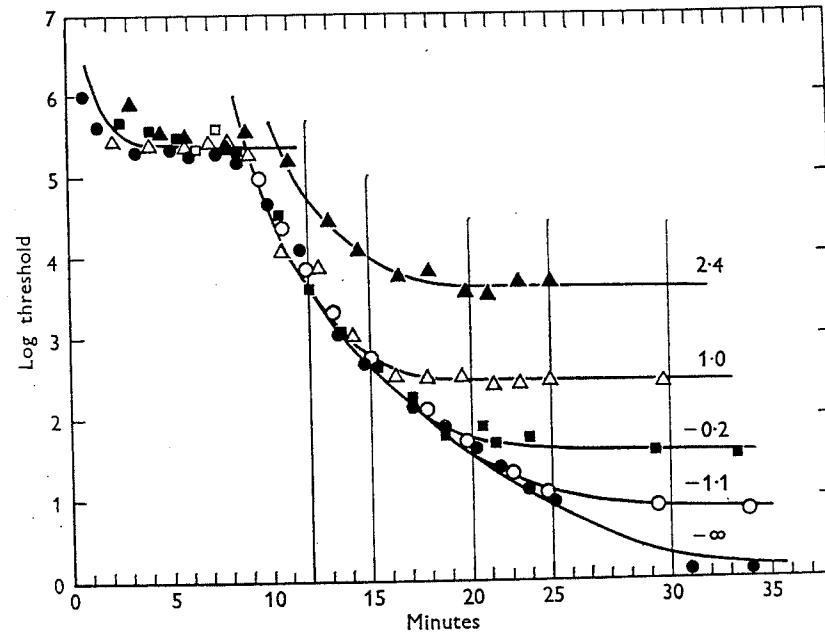


FIG. 7. Dark-adaptation curves of a subject deficient in cone vision. The test stimulus was added to a background field the intensity of which is given ($\log td$) by the number against each curve. The result cannot be accounted for by a change in quantum-utilizing power [F in Eq. (2)], but fits in with the idea that dark adaptation is caused by a declining dark light or intrinsic noise level [X in Eq. (2)]. (From Rushton, 1961b.)

is proportional to the fraction of rhodopsin bleached. We must conclude that bleaching a fraction r of the rhodopsin causes dark light to be increased by a factor that is proportional to e^{cr} ; c is a constant that Rushton's (1961b) results on a rod monochromat suggest has a value of 58. For the rods of rats that Dowling studied the constant would be much lower, and for cones (Rushton, 1959) lower still.

4.7 Possible Sources of Intrinsic Noise or "Dark Light"

It has been shown that intrinsic noise is likely to be an important limiting factor at absolute threshold, that variations of such a quantity aptly describe the major difference between rods and cones, and the

we shall tentatively assume that the thermal breakdown of photopigments is a limiting factor.

5.1 Size

The larger the eye, the bigger the pupil, and the more quanta it catches: hence a large eye should be able to achieve good intensity discrimination at a lower luminance level than a small eye. Note, however, that the advantage as regards absolute sensitivity is not so great. If all dimensions are increased, the retinal area covered by the image of an object increases to the same extent as pupil area. If retinal noise per unit area is the same in two species, the effect of increasing the number of quanta caught in the larger eye will be partly offset by the increased amount of retinal noise from the larger area of the image. The advantage of size is not completely nullified because the noise, being the root mean square value of the fluctuations, will only increase as the square root of retinal area, whereas the signal increases directly with pupil area.

5.2 Shape

Consider the aperture, defined as the ratio of lens diameter d to focal length f . It is an increase of d that increases quantum catching, an increase of f that, indirectly, increases retinal noise. The expected effect of these on absolute and differential threshold are given in Table I.

Small eyes tend to be starved of quanta at luminance levels which are adequate for bigger-eyed animals. This is presumably the selective factor lying behind Haller's law, which states that small animals have disproportionately big eyes. The smallness of an eye can be partially offset by increasing its relative aperture, and this is a fairly definite tendency in small eyes. However a more complete understanding of the situation requires a consideration of diffraction and chromatic aberration (see Section 7.2).

5.3 Transmission of Media

It is estimated that only about 50% of the light incident on the cornea reaches the retina in man. As pointed out by Pitts (1959) a reduction of this loss would appear to be wholly advantageous. It is in fact found to be less in cats, rabbits, and steers and the estimates on man may possibly show too high a light loss.

5.4 Density of Pigments

At first it might be thought that the more pigment the receptors contained the more quanta would be caught, with consequent lowering of

TABLE I
EYE SIZE AND VISUAL PERFORMANCE^a

Type of performance	Determining factor	Effect of dimensions at the limit ^b
Threshold intensities	Quantal fluctuations	Increment threshold $\propto \frac{1}{d}$
	Intrinsic retinal noise	Absolute threshold $\propto \frac{f}{d^2}$
Spatial and temporal resolution at low luminance	Quantal fluctuations	Resolvable angle or interval $\propto \frac{1}{d}$
Minimum resolvable angle at high luminance	Diffraction	Resolvable angle $\propto \frac{1}{d}$
	Chromatic aberration	Resolvable angle $\propto \frac{d}{f}$
	Receptor size	Resolvable angle $\propto \frac{b}{f}$

^a The table shows how performance depends upon eye dimensions, assuming the various stated factors determine the limit. Note that for all types of performance the larger eye has the better performance, except where chromatic aberration is the factor limiting acuity. If aperture is adjusted so that chromatic aberration matches diffraction, then $d \propto f^{1/2}$: small eyes need greater apertures for optimum acuity as well as for catching more quanta. For such an eye, resolvable angle $\propto 1/f^{1/2}$, as well as $1/d$. If receptor size is matched to image detail, $b \propto f^{1/2}$; small eyes need small cones.

^b d = pupil diameter, f = posterior nodal distance, b = receptor size.

physical limits to discrimination. But if the photic reaction occurs thermally, then an increased quantity of pigment is not without its disadvantage, for noise (root mean square fluctuation of spontaneous activation rate) increases with the square root of the quantity of pigment. Increasing the density of the pigment still brings an advantage, but only up to values where self-screening is important.

5.5 Disposition of Pigments

There are, however, other ways of increasing the amount of light caught by a fixed quantity of pigment. These are:

1. Orientation of molecules so that light passing down the rods is maximally absorbed, but polarized light with its electric vector lying parallel to the long axis of the rod is not absorbed at all. Schmidt (1938) discovered that rhodopsin was so arranged.

2. Reflection back down the rods. An enormous variety of reflecting

changes in threshold during dark adaptation. What can be said about its physical origin? And are there any physical limits to its value?

One can make a long list of possible origins, from radiant thermal energy in the eye to "mistakes" at a cortical level. The level of radiant energy can be calculated and its effects estimated by reasonable extrapolation: the result suggests that this is unimportant. Events at cortical levels may contribute to errors, but the fact that intrinsic noise can be described so nicely in terms of uniform dark light weighs against this interpretation. Three possible sources that fit what is known about intrinsic noise are: synaptic noise, accidental rod triggering, and thermal activation or breakdown of visual pigment. Not enough is known about the first two sources for us to assign any limits to them, but the third is a physical process some of whose properties are calculable.

4.8 Rate Required

The dark light of the human parafovea is equivalent to a light of $507 \text{ m}\mu$ sending in about 1,000 quanta/sec¹ deg² (Barlow, 1957a). Of these about 10% would be absorbed, and one square degree of retina contains some 10^{12} molecules of rhodopsin. Therefore, if thermal activation accounts for the dark light, an average of one molecule per second out of 10^{10} undergoes the same change thermally that is caused photically when it absorbs a quantum. This gives the maximum permissible rate, where thermal activation accounts for all the noise. Corresponding as it does to a half-life of some 220 years (at a temperature of 37°C) we see that rhodopsin must in any case be rather a stable molecule. Denton and Pirenne (1954a) reached a similar conclusion from calculations based on the threshold for a large, continuously exposed field. Their figures allow a somewhat shorter half-life, but in either case it is clear that a rate for the thermal reaction which is chemically insignificant is physiologically highly important.¹ For the cone pigments, the half-life would be shorter, probably about one month if the effective molecular absorption is similar to rhodopsin (but see Section 5.5).

It is interesting to speculate on the possibility that Crawford's increased dark-light of light adaptation is caused by decreased thermal stability of the visual pigment in the presence of surplus opsin: if so,

¹ Hubbard (1958) has shown that the bleaching reaction occurring *in vitro* at elevated temperatures leads to 11-cis retinene and opsin, unlike the photic reaction which leads to all-trans retinene. This interesting finding shows that a thermal reaction occurs which is unlike the photic reaction, but Hubbard would not have detected small quantities of thermally produced all-trans retinene. Hence her result does not rule out the possibility that the photic reaction occurs at the slow rates here postulated, and she is incorrect in implying that it does.

Rushton's figures show that when about 10% rhodopsin is bleached there is a 330-fold increase in the rate of the thermal reaction. Even at this latter rate, its half-life would still be about eight months at 37°C. Such an explanation would fit the facts rather well, but a physical mechanism has not been suggested whereby bleaching a little of the rhodopsin would render the remainder less stable.

Unfortunately the maximum possible thermal stability for a photosensitive pigment cannot be calculated with any confidence, but one can calculate how the rate of breakdown will change with temperature. So far, tests of this prediction have given negative results (Denton and Pirenne, 1954b), but it is not clear that the particular photic response chosen in that case was noise-limited.

The dependence of thermal breakdown rate on the activation energy is also known. The peak absorption of a pigment is related to the activation energy of the reaction initiated by light, and the expected dependence of thermal breakdown rate upon spectral absorption will be considered in Section 5.6.

4.9 Conclusions

We can summarize this section on noise by saying that it is expected theoretically and can be measured as the "dark light." Whatever the cause of "dark light" or intrinsic noise, it is necessary to use it to describe adequately the different performance of rods and cones, and the way sensitivity increases during dark adaptation. No known facts are inconsistent with the idea that it is caused by molecules of visual pigment undergoing thermally the same change that they undergo photically: only very low thermal rates are required on this hypothesis.

5. Instrumental Factors Limiting Measurements

Quantal fluctuations and noise limit the accuracy of measuring the quantities of light in the separate subdivisions of the image, but these factors by themselves do not determine the best possible performance of the eye in terms of discriminating objects in the environment. The pupil size and focal length of the eye influence the quantity of light entering and the retinal area it is spread over. The transparency of the media, and the density and the spectral absorption curves of the photosensitive pigments, determine the number of quanta absorbed. The influence of these factors on the overall performance will be considered in turn now, reserving for the next section additional factors connected with the efficiency of the eye in splitting up the light, and in collecting together and comparing the amounts in the separate parts. In the following discussion

tapeta has been evolved in different species (Walls, 1942), and these use a great variety of methods of procuring a high reflectance (e.g. riboflavin crystals in the lemur, see Pirie, 1959).

3. Channeling. If light striking a certain cross-sectional area of the retina can be concentrated into a smaller cross-sectional area, then a given quantity of pigment located at the latter position will absorb more of the light, with consequent advantage. The Stiles-Crawford (1933) directional-sensitivity effect may be due to some such mechanism in the cones. Tansley and Johnson (1956) have evidence that it occurs in the cones of the grass snake, and Rushton (1956a) found evidence for it in human rods.

5.6 Spectral Absorption Bands

The sensitivity of photographic plates was enormously improved by the addition of sensitizing dyes that extended their effective waveband towards the red end of the spectrum. Paradoxically, the eye does just the opposite when it adjusts itself for maximum sensitivity. The Purkinje shift occurs, and not only is the effective waveband curtailed in the red end, but the peak shifts over from near $560\text{ m}\mu$ to near $510\text{ m}\mu$. A similar shift, from about $585\text{ m}\mu$ to $525\text{ m}\mu$ occurs in animals possessing photopigments based on vitamin A₂ aldehyde. There is plenty of light available at longer wavelengths, and it seems at first strange that animals have not evolved pigments capable of utilizing it at low luminances, when it is most needed.

Once again the picture changes if one considers the possibility that thermal activation of photopigments limits their usefulness. The peak of a pigment's absorption band is related to the activation energy of the first change occurring when light is absorbed, for if the quantum contains insufficient energy, it cannot initiate the change and cannot be absorbed. There is not however a sharp lower limit, because the size of the smallest acceptable quantum is momentarily reduced when the energy of the molecule is momentarily high as a result of the fluctuating thermal bombardment. The expected law of decline of sensitivity on the long wavelength side of the peak is calculable from Boltzmann's distribution law on the foregoing assumptions. The theoretical expectation is that $\log_e(\text{sensitivity}) = \text{Constant} + h\nu/kT$, where h is Planck's constant, ν the frequency of the light, k Boltzmann's constant, and T the absolute temperature. Experimentally the decline is nearly linear, and inversely related to absolute temperature, as predicted. Its gradient is rather less than expected, but the theoretical treatment outlined above is certainly too simple. Lewis (1955) has applied a more exact theory, and obtains theoretical curves that fit nicely.

This result shows that the change occurring when light is absorbed can be aided by thermal energy and can presumably occur occasionally without light. Unfortunately, however, one cannot find how often this happens by extrapolating the curve to zero frequency (or the frequency of the ambient thermal radiation). Several factors make such an extrapolation unreliable, and in any case it would only give the fraction of the molecules with the required energy for activation at any one instant, not the fraction reaching it within a certain time.

It is reasonable, however, to ask what effect changing the activation energy, (and hence shifting the spectral sensitivity curve) will have on the thermal activation rate assuming all other factors are unchanged. The effect is remarkably big: for example if the activation energy is increased sufficiently to move the peak of the absorption curve from $560\text{ m}\mu$ to $507\text{ m}\mu$, the thermal activation rate would be expected to decrease by a factor of 4,200 (Barlow, 1957b). This is in fact rather close to the experimentally determined ratio of dark lights of scotopic and photopic systems, though it should be pointed out that the individual components of the photopic system do not behave as predicted according to this theory—Stiles's π_4 and π_5 mechanisms have roughly equal dark lights (Barlow, 1958b).

The idea that the thermal breakdown of photopigments is an important factor limiting visual performance has been employed in the foregoing discussion in spite of the absence of a direct experimental demonstration of its truth. But the hypothesis does get indirect support from the fact that it provides an explanation for several observed features of eyes; without intrinsic noise, the selective advantage of these features is unaccounted for.

6. Splitting up the Light

The light entering the eye is split up into separate subdivisions according to its direction of entry, its time of entry, and its color. There is little that can usefully be said at present about the physical limits of temporal resolution and color discrimination, except that the quantities of light in the subdivisions are small, and inversely related to the fineness of the splitting up. Hence it would be appropriate to consider the quantum and noise limitations in connection with tests such as flicker-fusion-frequency and wavelength discrimination (see Bouman, 1961).

The wave nature of light sets a limit to the fineness of subdivision according to direction of entry which is considered in this section. Chromatic aberration and receptor size define two instrumental limits which will be considered in Section 7.

6.1 Importance of Light Waves at the Limit of Acuity of the Eye

The wave structure of light limits the accuracy with which it is possible to determine its direction of incidence. Suppose that a distant point source is located exactly on the optic axis of the eye and then ask the question: "How small a displacement from the optic axis can be detected"? To see how waves limit the performance of this task, consider an analogy.

The regular ocean swell is entering the Golden Gate in San Francisco exactly at right angles to the line of the bridge. The task is to detect a small change in the direction of entry, without looking at the water west of the bridge. Initially the whole sea surface below the bridge rises and falls synchronously because the line of the bridge is parallel to the wave front. But if the direction of entry changes the rise and fall occurs earlier on one side, and there is an increasing phase difference as one moves across the bridge to the other side. For small changes of direction of entry, the maximum amount of phase difference will be directly proportional to the angle of change θ and to the distance across the harbor mouth d . For a given change of angle of entry, it is also clear that the phase change across the bridge will be inversely proportional to the wavelength λ of the swell. Now if it is supposed that a certain phase change is required before a change in direction of entry is detectable, then it must be concluded that

$$\theta_{(\min)} \propto \lambda/d$$

Though in an optical instrument the phase change across the entrance aperture cannot be observed directly, it is nonetheless this phase change that causes displacements of the image, and the above considerations apply. The same formula will hold, $\theta_{(\min)}$ now being the minimum detectable change in angle of entry, λ the wavelength of the light, and d the diameter of the entrance pupil.

The question exactly how big a phase change is required is more difficult to answer, for it depends upon what test is envisaged. If, as in the example above, we consider comparing the situation with a distant star exactly on and just off the optic axis, then it would be possible to detect a very small change—indeinitely small if the accuracy of measurement of intensities is indefinitely high. The situation usually considered is where we have to distinguish between one star, and two stars close together. A textbook of optics must be consulted for the derivation of this, the Rayleigh limit. For a circular lens aperture, the result is

$$\theta_{(\min)} = \frac{1.22\lambda}{d} \quad (3)$$

where λ and d are in the same units and θ is in radians. It should be pointed out that this is not a true limit, for the images of a single star and a pair do not become identical when θ is below the limit. They simply differ by less than an arbitrary amount, but recent developments have removed this arbitrariness. Let us see how well the eye's own optics do in comparison with this value.

6.2 Diffraction and Human Acuity

For two point sources the minimum resolvable angle for the human has been taken since the time of Hooke to be very close to 1 minute of arc. Calculations from Eq. (3) show that this requires a pupil diameter of 2.35 mm (taking $\lambda = 560 \text{ m}\mu$). The pupil is normally a little larger than this, but we can see at once that acuity approaches quite close to a limiting value set by the wave nature of light. The same conclusion applies for grating test objects (Shlaer *et al.*, 1942). Nor is this a mere accident applicable only in the case of the human eye, for we shall see that it also applies in a radically different case, the compound eye of insects.

6.3 The Compound Eye

Compound eyes have many separate optical systems each pointing in a slightly different direction. It is probable that spatial discrimination is achieved by comparing the amounts penetrating each ommatidium to the level of the photosensitive cells, and the resolving power therefore depends both upon an anatomical factor, the angle between neighboring ommatidia, and upon a physical factor, the ability of each ommatidium to confine its lobe of directional sensitivity so that it does not overlap those of its neighbors too much. It is possible that in certain insects the seven or eight sense cells of each ommatidium may have different lobes of sensitivity, but this does not greatly affect the following argument. The theoretical limit to the narrowness of a lobe of directional sensitivity is set by diffraction at the entrance to the ommatidium. These have a diameter of about 22μ in the honeybee, for which the limiting resolution would be 96 min.

If there has been evolutionary selection in favor of good acuity, then we should expect the eye to evolve so that the anatomical factor, interommatidial angle, is just not limiting—i.e., interommatidial angle in the bee should be just below 96 min. One finds that this is in fact the case, the smallest interommatidial angle being about 58 min (Mallock, 1894, de Vries, 1956; Barlow, 1952). Though this is encouraging, a single coincidence is not too impressive, and one can easily enough find cases where

the interommatidial angles are much greater than the limiting theoretical resolution of individual ommatidia.

For a more convincing demonstration that evolution has here reached a physical barrier we must consider a range of eyes of different overall sizes. As the eye size is reduced, either the number of ommatidia must be reduced, or the size of the ommatidia, or both. The considerations outlined above lead one to expect that in an ideal compound eye both will be re-

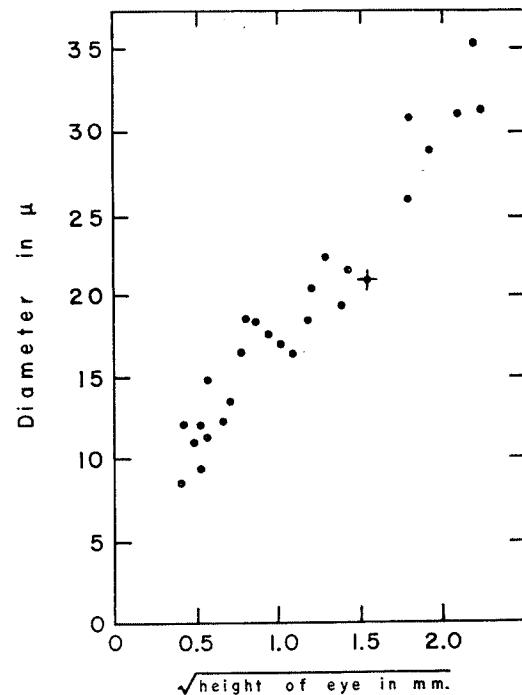


FIG. 8. Diameter of ommatidia in 27 species of Hymenoptera. If the design were optimal, the anatomical limiting factor (interommatidial angle) would be matched to the physical limiting factor (diffraction in each ommatidium). In that case ommatidial diameter would be proportional to the square root of the eye size, and this is seen to be roughly true. (From Barlow, 1952.)

duced equally to maintain the balance between diffraction and interommatidial angle. In this case, the ommatidial diameter will vary in proportion to the square root of the overall linear dimensions of the eye (Barlow, 1952). To test this prediction, in Fig. 8 the ommatidial diameter in microns has been plotted against $\sqrt{(\text{height of eye in millimeters})}$ for 27 species of Hymenoptera. These were diurnal species varying in body

length from 1 to 60 mm, in eye size from 0.2 mm to 5 mm, and in ommatidial diameter from 8μ to 35μ . The point for the honeybee is indicated by a cross. Ideally one would expect the points to lie on a straight line through the origin, and although there are slight deviations from this expectation, the results certainly tend to support the conclusion that evolution has molded these insect eyes to do the best that wave optics allows.

7. Chromatic Aberration

Diffraction has been considered in Section 6. If this were the only limiting factor, then acuity would improve linearly with pupil diameter, and one would expect eyes to be evolved with very large relative apertures. But at wide apertures optical errors tend to spoil the image, and of these chromatic aberration is probably the most important. There is no evidence for any type of optical achromatization, though lens pigmentation (Kennedy and Milkman, 1956), the yellow macular pigment, and colored oil droplets in the receptors of birds, must have the effect of narrowing the spectral sensitivity curves and thus reducing the intensity of the chromatic fringes. But with broad receptor spectral sensitivity curves chromatic aberration is bound to mar resolution.

Calculation suggests that in man chromatic aberration, like diffraction, is an important factor in blurring the retinal image. Hartridge (1918) estimated that for a 3-mm pupil the image of a point source would be spread so that 76% of the luminous flux would fall within a disk of radius 45 sec of arc. This was for the artificial and unrealizable case of chromatic aberration alone: diffraction alone would, with a 3-mm pupil and $\lambda = 560 \text{ m}\mu$, spread the light so that 84% fell within 47 sec of arc of the center point. At this pupil diameter diffraction and chromatic aberration are therefore of roughly equal importance. At bigger diameters, the effects of chromatic aberration will predominate whereas at smaller diameters diffraction will predominate. It is hard to calculate the combined effect of chromatic aberration and diffraction, but Westheimer and Campbell's (1962) experimentally based result suggests that if other factors are present, they are not enormously important. They estimated that the light intensity in the image of a point source of white light drops to one-half its peak value at a distance 40 sec from the center, with 3 mm pupil.

7.1 Scaling Laws for Acuity

If an instrument whose resolution is limited by diffraction alone is doubled in size, the minimum resolvable angle is halved. But in an instrument like the eye this improvement would not be attained. Chromatic

aberration sets a limit which depends only upon the relative aperture of the optical system (assuming dispersion constant) and is independent of absolute size. Hence a simple scaling up or down would not maintain the balance: diffraction would limit performance in small eyes, and chromatic blurring would limit it in big eyes. To maintain this balance, the focal length should be increased in proportion to the square of the pupil diameter: relative aperture should be decreased in big eyes, increased in small eyes.

These relations, together with those concerning sensitivity, are summarized in Table I. It will be seen that there are two factors favoring the wider relative apertures which tend to be found in small eyes. First is the shortage of quanta. Second is the fact that the reduced absolute size of pupil lowers the diffraction-limited acuity, and this in its turn allows the relative aperture to be somewhat increased until chromatic aberration balances diffraction again.

7.2 Retinal Resolving Power

Details in the optical image would be of no benefit to an animal if the retina was incapable of signaling them centrally. It is no surprise to find that the cones in the fovea are adapted in size to this detail—at least approximately. A nice experimental demonstration of the way the retinal resolving power is matched to that of the optics was given by Westheimer (1960) who cast on the retina a diffraction image the quality of which was largely unperturbed by optical imperfections of the eye. He was thus able to test the resolving power of the retina alone, and found that it was substantially the same as the best that the eye can do using its own optics. But we have just seen that diffraction prevents better resolution if the pupil diameter is below 2 mm, and at apertures of about 4 mm and higher chromatic aberration is predominant. In the range of pupil size used at high luminances, all three factors are matched and about equally important.

The receptors are probably the anatomical factor limiting retinal resolution and it is natural to ask how their size should be varied to maintain balance in eyes of different dimensions. It turns out that the size of the cones should be inversely proportional to the relative aperture of the eye. This follows from the fact that the angular resolution is proportional to lens diameter, and the image size is proportional to focal length. Hence the linear dimension of the smallest resolvable detail is inversely proportional to relative aperture, as in the limit to resolution of a microscope objective. Apparently a small eye, with relative aperture increased to maintain balance between chromatic aberration and diffraction, re-

quires smaller cones to resolve the image. The smallest cones should be found in small eyes adapted to have high acuity.

7.3 Role of the Pupil

So far the size and shape of the eye have been discussed without any reference to the fact that its aperture can be varied by the pupil. The surprising assortment of mechanisms which change the shape as well as the area of the entrance aperture are described by Walls (1942). Obviously the reduction in area in bright light and its increase in dim light tends to reduce the variation in retinal illumination, but if this is its main task it is surprisingly inefficient at it (Stark and Sherman, 1957). A millionfold change in the light entering the eye causes only a tenfold change in pupil area, and hence the variation in retinal illumination is only slightly reduced.

If the other factors that limit ocular performance are borne in mind this becomes less surprising. Excessive narrowing of the pupil aperture would mar acuity by diffraction, and this must set a lower limit to the useful aperture. As the luminance level is reduced the pupil can dilate, but if it dilates too far then chromatic and other aberrations would mar the image quality sufficiently to offset any gain in resolution resulting from the increase in image luminance. Thus for any luminance level there would appear to be an optimum aperture below which resolution is limited by low image luminance, or by diffraction, and above which it is impaired by optical aberrations. The observations of Campbell and Gregory (1960) support this interpretation of the change of pupil diameter with luminance in the human eye.

7.4 Restricted Value of Deductions from Physical Limits

It will be evident that this "design study" for eyes can only lead to broad expectations. One would not expect scaling laws deduced for acuity to apply to a nocturnal animal, nor scaling laws for cone size to apply in the peripheral retina, where the acuity is far below the optical limits. The physical considerations only give limits to size and performance. Selection pressure, which is governed by complex biological factors, will determine how closely the limits are approached. Furthermore the physicist takes biological data for his starting point—the general plan of the eye, simple or compound, and the type of discrimination performed. But the biologist will have a very incomplete picture of the evolution of the eye unless he is aware of the physical limits, for they are barriers that no amount of selection and mutation can overcome.

8. Collecting, Comparing, and Deciding

8.1 General Discussion

The task of extracting information about the environment has only been started when the light has been split up and responses initiated that are graded according to the amounts in each part. In real life the objects in the visual field that have to be discriminated from their background are usually larger, and persist for a longer time, than the smallest of the subdivisions. The physical limit to performing a discrimination depends, not on the amount of light in the smallest subdivisions, but on the total amounts in the parts of the field that are to be discriminated from each other. Being much larger quantities, the discrimination can be much finer, but to achieve this in practice requires arrangements for adding together the amounts in these parts. Thus the way, or variety of ways, in which the visual system is able to summate, integrate, or collect together the signals from the separate small parts for purposes of comparison and decision, is important in determining how closely it approaches the true physical limit.

Very complex problems are involved here, as can be shown by briefly considering a "retina" of ten cells, each either "on" or "off." The result of a "decision" is "yes" or "no," and there are 2^{20} ways in which such a decision can be made about input patterns (because there are 2^{20} functions of ten binary variables). If we suppose, as we must, that some ways of making the decision cannot be realized by the "brain" connected to the retina, then the system will be inefficient at performing certain discriminations: it will extract information about the environment less efficiently than it might. To illustrate this in a simple case the effect of a particular limitation will be discussed. These effects are, in theory, calculable, but the discussion will also show that an important piece of neurophysiological information required for this calculation is missing.

8.2 Effect of Summating Pool Area

We know that the ganglion cells of the retina "pool," or collect together, all the light falling in the excitatory parts of their receptive fields. These integrating pools are of different sizes in different ganglion cells, and the size varies systematically in different parts of the retina (Hubel and Wiesel, 1960). Let us see how the size of the integrating pool affects the performance. This is more complicated than the problem of calculating the ultimate physical limit, but the retina is really yet more complicated, for ganglion cells are inhibited by light as well as being excited: apparently some of the comparison, as well as the collecting, is

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done in the retina. However here we shall only go as far as working out the effect of a mismatch between the size of the pooling area and the size of an object in the visual field which, we suppose, has to be discriminated in intensity from a large uniform background. The problem is simplified by assuming that, because this is large and has been seen for a long time, its intensity is accurately known: the only limiting factor is inaccuracy in measuring the intensity over the area of the object. We simplify the problem by supposing that the object is the only unknown quantity. Thus the problem is exactly the same as for the increment threshold (Section 3), the background being at intensity I , and the object at intensity $I + \Delta I$.

Suppose the image of the object covers a retinal area A , and the "pool" of the ganglion cell is of area α . Now if $\alpha = A$, and if the image exactly fills one pool, then that particular ganglion cell collects all the light from the object, and only light from the object. It should, then, receive information about the exact number of quanta absorbed, limited only by possible inaccuracies in transmitting this information from receptors to the ganglion cell; except for such inaccuracy, it should reach the physical limit of Eq. (1).

If $\alpha > A$, then a ganglion cell can receive all the light from the object, but it is bound to receive light from the background as well. Under these conditions the incremental quantity of light, $\Delta I \cdot A$, will be constant: hence the threshold difference in intensity, ΔI , should be proportional to $1/A$. This law (Ricco's law) is in fact found for small stimuli, and one can tentatively identify the size of the pool, α , as the highest value of A for which $\Delta I \propto 1/A$ holds. Notice that ΔI is higher than it would have been if α had been reduced with A , for then the true physical limit, where $\Delta I \propto 1/A^{1/2}$, would have been reached.

Rather different considerations apply when $\alpha < A$. Here no single ganglion cell receives all the light from the object, and hence no cell at this level receives information as to how many quanta were received from the object. For a single such cell, the "threshold" intensity would remain constant and independent of A , once this was greater than α . However we do not know that ganglion cells have "thresholds": they might signal the exact number of quanta absorbed in their receptive field to a cell in the lateral geniculate body or cerebral cortex which also received connections from all other ganglion cells covered by the image of the object. Such a higher-level cell would then receive accurate information as to the total number of quanta absorbed from the object, and might make a discrimination up to the physical limit. In this case, the limit is $\Delta I \propto 1/A^{1/2}$, and it is interesting that this law (Piper's law) does hold over a considerable range when the area is greater than that for which $\Delta I \propto 1/A$, provided

that the background light I is low. Notice, however, that there is an additional step involved here, compared to the other efficient case where $\alpha = A$, namely the signaling of the number of quantal absorptions from each ganglion cell to the higher-level nerve cell. The higher-level cell's estimate of the number of quantal absorptions is subject to additional inaccuracy from errors occurring here. This is of interest in view of the fact that $\Delta I \propto 1/A^{1/2}$ ceases to hold when light stimuli are added to an increased intensity of background light, which suggests that ganglion cells can accurately signal small numbers of quantal absorptions, but become inaccurate when the numbers are large.

This discussion of the effect of pooling area upon the efficiency of discrimination leads to the idea that efficiency will be greatest for a particular area of stimulus, and will decline for larger or smaller stimuli. Clark Jones (1959) has found such optima in measuring the quantum efficiency of vision for varying areas of stimulus. He also found an optimum duration, and it is clear that considerations similar to those outlined above for area will also apply to the integration time.

Enough has been said to show that the neural arrangements available for collecting and comparing the signals from the small subdivisions of the image are important in determining the physical limit. But the discussion has brought out an important gap in our knowledge. This is the nature and extent of the loss of accuracy occurring when nerve cells signal the amounts of light received in the receptors they are connected with. It is our ignorance about this that prevents us understanding better the relation between nervous organization and psychophysical performance.

9. Summary

Taking due account of quantal fluctuations, intrinsic noise, diffraction, and chromatic aberration helps one to understand the "design" of the eye, for these factors define limits that evolutionary adaptation can approach but cannot overcome. However one gets more than an improved understanding of known features of eyes by paying attention to these limits. One is given a new perspective on what particular properties of the eye limit its performance, and one's attention is directed to features that are performance-limiting but not well understood. In the following paragraphs some of the problems that are thus raised will be outlined. The six papers that raise these problems, and perhaps begin to solve them, will be mentioned by name, since they are the key references for anyone interested in the general topic of this chapter.

The classic paper by Hecht *et al.* (1942) on "Energy, Quanta, and Vision," showed that quantum fluctuations are an important factor at the absolute threshold. However, the fact that the increment threshold is

directly proportional to the intensity of an adapting light, rather than to its square root, shows that another factor enters to prevent the quantum fluctuation limit being reached when the eye is light-adapted. This is perhaps shown most clearly in Aguilar and Stiles's paper (1954) on "Saturation of the Rod Mechanism at High Levels of Stimulation," which also shows an abrupt cut-off of the rods at a high luminance. The cause of the loss of efficiency that progressively increases with adaptation level is one of the major problems raised, for under many ordinary conditions it is the main factor limiting performance.

Intrinsic noise, measurable as "dark light," is a useful concept to describe the different performance that rods and cones are capable of, and a declining dark light accounts satisfactorily for the change in performance during dark adaptation. This was shown up particularly by Crawford (1947). Dowling's paper (1960) on "The Chemistry of Visual Adaptation," and that of Rushton (1961b) on "Rhodopsin Measurement and Dark-Adaptation in a Subject Deficient in Cone Vision" relate the log of the change in threshold to the amount of rhodopsin bleached. The outstanding problem here, then, is "Why is the intrinsic noise proportional to exp [bleached rhodopsin]?"

With regard to spatial resolving power, diffraction and chromatic aberration are probably the major factors blurring the retinal image, but Westheimer and Campbell (1962) and Krauskopf (1962) in their papers on "Light Distribution in the Image Formed by the Living Human Eye" have described a technique that should enable this problem to be solved.

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Chapter 17

STUDIES ON ULTRAVIOLET RADIATION ACTION UPON ANIMAL CELLS

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Interest in the effects of ultraviolet (UV) radiation upon animal cells initially stemmed from the need for interpreting the effects of these radiations upon man, a point of focus in Finsen's Light Institute in Copenhagen where, in fact, some of the first basic studies of the effects of UV radiation on animal cells were carried out (Dreyer, 1903, 1904; summary in Busck, 1904). Because of the complexity of human skin such studies early centered upon such cells as protozoans, blood cells, and cells in tissue culture (Puck, 1957), most of which could be obtained in suspensions and so could be irradiated singly or in single layers, and were considered to have a greater resemblance to the cells of man than bacteria.

It was soon realized, moreover, that animal cells present opportunities—sometimes unique—for the analysis of problems of irradiation not as easily studied in bacteria. For example, if the immediate changes in division rate after irradiation are to be followed, animal cells in suspension, since they are larger, are more suitable than bacteria because each event in division may be observed in an isolation culture. It is also possible to follow chromosomal changes during mitosis and meiosis (Carlson, 1950), to irradiate only a portion of a cell, an organelle, or even a small part of an organelle such as a kinetochore of a chromosome (Zirkle, 1957). Changes in responsiveness of cells, and of their motility after irradiation as well, are more effectively studied with animal cells.

1. Direct and Indirect Effects of Ultraviolet Radiation

The effects of radiation on cells, such as the modification, injury, or death of the cell, could result from a direct effect of the radiation upon

¹The effects of UV radiation on biological macromolecules and their bearing on the mechanism of UV action in cells are dealt with in Chapters 2, 3, 4, and 20. The mutagenic action of UV radiation is considered in Chapter 18. The biochemical reactions in animal and microbial cells which are affected by UV radiation, and their photoreversal, are discussed in Chapter 19.