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Retinal and Central Factors in Human Vision Limited by Noise

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When I started research in vision, Rose and de Vries’ papers(1) had just appeared, and it was an enormously attractive thought to me that the limiting performance of the eye could, under many conditions, be accounted for simply by the quantum fluctuation of the absorbed light. Now the simplest prediction from such a hypothesis is that increment threshold ΔI will increase as the square root of background luminance I. Though ΔI usually rises more rapidly, conditions can be found where this Rose-de Vries Law, ΔI ∝ I^{1/2}, holds well over a wide range of background luminance.(2) This occurs when the test stimulus is of small area and short duration, and the suggested explanation is, of course, that the quantum fluctuations of the background are proportional to I^{1/2} and set a lower limit to the number of quanta that can be detected from the test flash. For this to be a valid explanation the light must be summated over a fixed area and time, but unfortunately this is probably not true; over the range where the square root law holds, the product of summation time and area is approximately proportioned to I^{-1/4}.(3) It is therefore hard to accept that the Rose-de Vries hypothesis, in its elementary form, is the explanation of the Rose-de Vries law.

Another way of stating the Rose-de Vries hypothesis would be to say that the quantum efficiency is constant. Rose(4) has very forcefully stated the case for this, and it is obviously a useful guide to instrument designers and others to be told that quantum efficiency stays between 10% and 1% over a wide range.
of mean luminance of the visual scene. However to those interested in how the eye works, the concept of quantum efficiency is chiefly of interest in leading one to factors other than quantum fluctuations that limit performance. To use the concept this way, one finds where quantum efficiency declines, for that is where the other factors enter. It is thus not surprising that my emphasis is on its lack of constancy, whereas Rose and others emphasize its constancy.

It is also, for the physiologist, particularly important to stick to a strict definition of the overall quantum efficiency of visual performance. It is the ratio of numbers of quanta required by an ideal device to the number required by an actual subject performing exactly the same task. To simplify the calculation for the ideal performance, unjustified assumptions are sometimes made about the way the eye performs the task.\(^{(4,5)}\) The eye, considered as an instrument, has many tricky design features, and it is by no means safe to assume that it can be characterized by a few simple parameters, or that one knows what they are. One can detect a highly redundant stimulus, such as a flickering light or a grating, when the elements of which it is composed (a single flash or a single bar of the grating) are far below the limit of visibility. Also, partial summation continues well beyond a summation parameter defining a reciprocity limit. There are also likely to be parallel pathways with different parameters subsuming different detection tasks. For such reasons the eye may seem to have a higher quantum efficiency than is in fact found to be the case when measurements are critically conducted.\(^{(5)}\)

In spite of these difficulties it is a useful tool to explore how much we actually know about the factors limiting vision, and in this paper I propose to review estimates of the fraction of quanta absorbed (absorptive or photometric quantum efficiency) and compare them with the best measurements of the quantum efficiency of visual performance of the whole organism (psychophysical or behavioural quantum efficiency), or of a neurophysiological preparation.

Psychophysical and Photometric Efficiencies

The situation at and near absolute threshold will be considered since this is where there is the smallest gap between photometric and psychophysical quantum efficiencies, but the gap is not as small as it appeared to be when the original work was done. Hecht, Shlaer and Pirenne\(^{(6)}\) estimated that no more than 10\% of 507 nm light incident at the cornea was absorbed in the rods; their measured thresholds averaged 112 quanta at the cornea, so they concluded that a flash visible on 55\% of occasions caused, on average, about 10 quantal absorptions. They then showed that the slope of frequency-of-seeing curves was such that at least 5 quanta, and sometimes 8, must be utilized at threshold. They were well pleased with how close this figure approached the direct estimate of 10, and reached the physiologically satisfying conclusion that “biological variability” and “psychological factors” were not disturbing their measurements; quantum fluctuations were the dominant factor.

Now this argument rests heavily on that figure of <10\% for the fraction of corneal quanta absorbed. It was reached by a beautiful and judicious argument that brought in many facts no one else had considered, but I think the conclusion is undoubtedly wrong, perhaps by as much as a factor of 3. Table 1 shows the most judicious estimates I can now make. The main factor

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<td>Photometric, psychophysical and neurophysiological estimates of the proportion of quanta at the cornea that excite rods. For fuller discussion of the factors see references 18, 21</td>
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<td><strong>Photometric</strong></td>
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<td>Human absolute threshold assuming noise (X_r = 0)</td>
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<td><strong>Neurophysiological</strong></td>
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<td>Cat retinal ganglion cell Measured (X_r = 10)</td>
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that has changed is the figure for absorption in the receptors in the third line, which Hecht et al. thought was under 20\%. The figure of 50\% or more given here is that derived by Alpern\(^{(7)}\) and colleagues by several methods, and I think it is strongly supported by the results of Marks\(^{(8)}\) and Liebman\(^{(9)}\) on photometry of single photoreceptors. (See also MacNicholl’s discussion of Rose's paper: this volume, p. 12.)

A factor which has changed in the other direction is the fraction exciting, in the fourth line. It is usually assumed that only quanta causing isomerization can excite, and I have therefore included the factor of 0.6.\(^{(10)}\) But we do not know this for certain; even without isomerization the energy from the quantum is locally available, and the amount is comparable to the mechanical energy of a threshold acoustic stimulus.\(^{(11)}\) Even if it does not isomerize, it is all available in a single subcellular particle, whereas the threshold acoustic
stimulus is presumably spread out among many hair cells underlying the basilar membrane, presenting a much harder detection task.

I think one must admit the possibility that as many as 33% of quanta entering the cornea are available to excite rods, but you don’t have to believe the higher figure to be worried by the discrepancy between these estimates of photometric efficiencies, and the behavioural quantum efficiencies. In the bottom part I have summarized these. The figure for the human is obtained by taking the average threshold from the results of Hecht et al.,(6) namely 112 quanta, and dividing this into the average of the number of quanta utilized, obtained from the frequency-of-seeing curves, namely 6.

Now some estimates of human quantum efficiency above 5% have been published, but as mentioned earlier there has usually been a flaw capable of leading to spuriously high results. For example, invalid assumptions were made about the spatial and temporal integration of the retina; or the number of quanta involved was calculated for a single eye, whereas the psychophysical data were obtained with two; or the estimate of the signal/noise ratio of the human subject needed refinement. Hallett(20) developed a method to correct for drifts of sensitivity and obtained quantum efficiencies up to 10% by using this correction. However Hecht’s figure of 5–6%, subsequently confirmed by Baumgardt(12) and myself(5), is the highest one that is fully convincing.

Some psychophysical estimates below 5% have also appeared. Sakit(31) suggested that subjects looking at very weak flashes of light can give responses graded according to the actual number of quanta exciting rods, this number being thought to vary from zero to about 6 under her conditions. This explained many aspects of her data, and it required a dark light $X_s$ at the cornea (see below) of 10 to 40, and quantum efficiencies of about 3%. The latter figure is in acceptable agreement with other psychophysical estimates considering that she used 7° eccentricity, but $X_s$ is much lower than that estimated below. The weakness of her argument is that she cannot say “At most one, or two, or three... rod excitations were involved for the corresponding ratings”, whereas quantum efficiency arguments lead to firm limits. It therefore seems preferable to take 3% at 7° eccentricity as a minimum rather than as a definitive estimate.

Van Meeteren and Bougard(14) used an interesting method in which the efficiency is obtained by comparing a subject’s performance when limited by quantal fluctuations with his performance at a similar task when it is limited by the fluctuations of a random dot pattern within which the test pattern appears. It is a more quantitative version of Rose’s(11) original method. Their figure for rod vision is 1%, though it appears that the exact nature of the task performed affects the result, and 1% may not be the figure for an optimal task.

Also included in Table 1 is the result of estimates done on retinal ganglion cells in the cat. The figure given is the average for the 5 most sensitive ganglion cells out of 11 thoroughly studied and, in contrast with the human, this figure is compatible with the photometric absorption, though it is at the lower limit. Now there are two obvious differences between the cat and human estimates: first, the cat figure includes an allowance for intrinsic retinal noise; second, the cat method is done at a level preceding the central processing and decision making, and hence avoids any losses of efficiency incurred there.

The quantitative effects of visual noise and central inefficiency are pursued in the following sections of this paper.

**Intrinsic Noise**

Hecht et al.(6) matched their psychophysical data to a model in which a “seen” response was given if $c'$ or more quanta were absorbed, “not seen” if less than $c'$. When the frequency of seeing curves predicted by this model are plotted with log (stimulus intensity) as abscissa, the slope at $P = 0.5$ is approximately given by

$$dP(c' \text{ or more})/d \log I = c'/2 \log e - 0.5.$$  \hspace{1cm} (1)

Their experimental frequencies of seeing suggested values of $c'$ ranging from 5 to 8, averaging close to 6. It is also clear that, on their model, the 50% threshold $I = c'/F$ (approx.), where $F$ is the proportion of quanta at the cornea that is absorbed in rods and contributes to visibility. For their experiments $I$ averaged 112 quanta at the cornea, and hence the best estimates of $F$ from their results is $6/112 = 0.054$. By optical methods the proportion of quanta at the cornea that excite rods is now thought to be at least twice as high (Table 1).

It is now abundantly clear that there is noise in the retina, and this might account for the difference. The simplest way to explore its effect on visual performance is to introduce a new parameter $x$, which represents a number of random independent events liable to be confused with the effective absorption of a quantum of light.(15) It is true that this way of expressing noise rather suggests it is very peripheral in origin, for instance thermal isomerization, but wherever it occurs it should be possible to express it in this form to a first approximation, and it is the simplest way to express it if one is interested in its effect on visual performance. Figure 1 shows how a set of predicted frequency of seeing curves is generated by supposing a fixed criterion $c$ and varying $x$. These become flatter and shift to the left as $x$ is increased, in rather the same way that the set without noise (dotted curves) shifts and flattens as $c'$ is decreased. For instance, the curve for $c = 64$, $x = 40$ has a slope nearly equal to that for $c = 9$ without noise, whereas that for $c = 64$, $x = 50$ would be nearly equal to $c' = 3$ without noise. The experimental curves for Hecht et al., characterized by a slope for $c' = 6$, would require a noise of $x = 44$ if the
mean and slope, and as you see these depend on both \( c \) and \( x \). Clearly, to make any progress one needs an independent method of estimating \( x \).

One can obtain this as follows. Suppose the absolute threshold experiment is modified slightly. Stimuli are delivered containing either \( L \), or \( L + K \), quanta (on average), but instead of asking the subject if he sees the flash or not, he is told that "dim" (containing \( L \) quanta) and "bright" (containing \( L + K \)) will occur with equal probability, and it is his task to say which an unknown one is. He can see samples of the two classes whenever he likes, but whenever he receives an unknown he must of course classify it as dim or bright. When \( L \) and \( L + K \) are small, of the order of 100–200 quanta, this is very much like a threshold task, for the subject rapidly finds that he rarely sees the dim ones, so he classifies all the seen ones as bright. For higher values a subject can find a dividing criterion among the visible stimuli, and he is aided in doing this not only by samples of "dim" and "bright" obtained when required, but also by being told whether a judgement was right or wrong, thus receiving feedback.

We define \( K^* \) as the value of \( K \) which allows the two classes to be discriminated with a \( d' \) (or internal signal/noise ratio) of 1. As \( L \) is increased, initially \( K^* \) is little effected or may even decrease, but eventually \( K^* \) increases steeply. If \( L \) corneal quanta cause \( I \) absorptions, these will be added to \( x \), the noise events, and one can get information about the noise by finding the value of \( L \) at which it starts to impair detection of additional quanta.

Figure 2 shows the result for two subjects. It is hard to see any deleterious effect of \( L \) on \( K^* \) until \( L \) is greater than about 200 quanta in one subject, 300 in another. Define \( X_e \) as the number of quanta at the cornea that would cause \( x \) quantal absorptions. Then this result is incompatible with a value of \( X_e \) below about 200. However, one cannot press the accuracy of this result for the following reason. If the situation was simply as I've described it, \( K^* \) should increase as \( \sqrt{L} \) at high values, but clearly it goes up more steeply. Also the small but definite sensitization effect is unexplained. Nevertheless, if \( X_e \) was small, say about 10, then values of \( L \) in that range should affect \( K^* \), and they do not.

This type of experiment clearly suggests that \( X_e \) is of the order 200 or more, and this is also fully compatible with the value of \( I_o \), the "dark light" or "eigengrau", derived from increment threshold experiments. \( I_o \) was found to be about 1000 quanta s\(^{-1}\) deg\(^{-2}\) in a review of many such experiments,\(^{21}\) and if summation time and area are taken as 0.2 s and 1 deg\(^2\), this agrees well with the above result.

To find what this value of \( X_e \) implies about \( F \) one reasons as follows. The slope on the noise model (eqn 2) is equal to that determined experimentally by Hecht et al. (eqn 1) so we know that:

\[
\left( c - x \right)/c^{1/2} = \left( c' \right)^{1/2}.
\]
above value of $X_c = 200$, one finds that $F = 0.15$. Values of $F$ of 0.11 and 0.33, which are the lower and upper estimates of photometric efficiency in Table 1, require values of $X_c$ of 120 and 580, respectively.

My conclusion at this point is that intrinsic noise can account with reasonable quantitative accuracy for the difference between photometric and psychophysical quantum efficiencies. The notion of intrinsic noise was advanced with the idea that it originated somewhere in the retina, that is in the synapses or receptors or even by thermal isomerization of photopigment molecules. Some of the relations between psychophysical performance and visual noise as measured by $x$, $X_c$, or $I_0$ are discussed elsewhere in this volume following the reported measurements of the electrical noise of cones (reference 16; see also reference 17). However it would be wrong to assume that the high values of $X_c$ reported above arise solely in the receptors, as shown in the following section.

**Sources of Intrinsic Noise**

In a system with a noisy input it is pointless to reduce the noise of later stages far below that of the input for, owing to the fact that variances add, the largest source of noise dominates and smaller sources contribute a negligible amount to the total noise. Thus one may not get a clear answer to the question “What causes visual noise?” anymore than one does to the question “What limits acuity?” There is, however, mounting evidence that the high value of $X_c$ of 200–300 arrived at above is not all in retina in origin. For the cat retinal ganglion cell $X_c$ is only of the order 10, sometimes less. This was derived as follows:

The maintained discharge, and the variance of the maintained discharge, are both thought to be due to $x$, the events indistinguishable from quantum absorptions. If a stimulus flash is given, extra impulses are generated, and variance is increased. By extrapolating backwards one obtains estimates of $X_c$ at the intersection with the abscissa. The results from mean and variance are slightly different, and there is also a good deal of variability from cell to cell. But the average of the best 5 cells was 4.6, of all 11 cells 11.8. These are clearly very much lower than the human psychophysical estimate, namely over 200.

From those measurements one can also obtain an estimate of the quantum efficiency, which is given in Table 1. From that type of measurement one obtains estimates from 5% to 18%, but for the best 5 it averaged over 12%, which was the lower limit for photometrically estimated absorption in the cat (see Table 1).

The human periphery is not necessarily like the cat, but suppose it was: How then could one account for our estimate of $X_c = 200$? The answer is “Only too easily”, for so far no allowance has been made for imperfections of the central
mechanisms. Suppose, for instance, that central threshold, equivalent to the criterion number of events \( c \), fluctuates; the psychophysical methods do not readily distinguish between fluctuations of \( c \), and fluctuations of signal size resulting from the random fluctuations of \( x \), which were originally conceived as being purely retinal in origin. This means that the formal explanation in terms of intrinsic noise is rather hollow; without more information we don’t know what the noise is intrinsic to.

In Table 2 some of the possible sources of noise are listed, together with visual phenomenon that may be related. Obviously the methods of choice for getting information about the first four are now physiological, but recent work does bring out the very great importance of the fifth one. High level phenomena may have effects exactly like retinal noise, and what we thought was the latter may in fact be largely the former.

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<th>Table 2 Possible Sources and Effects of Intrinsic Noise</th>
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Threshold Variation and Central Efficiency

When one does measurements close to absolute threshold one is aware that funny things are happening. For instance, if one is to decide whether a stimulus belongs to a “dim” or “bright” class one would like to see many members of each class before deciding about an unknown. But this turns out to be a virtually impossible procedure, for as one repeatedly delivers the “bright” ones, they become invisible! At first one blames oneself for poor fixation, but paying attention to this shows that the stimulus reappears if you deliberately fixate \( \frac{1}{2} \) away from the correct fixation position. These effects are not small, they are very large, as has been shown by Frome, MacLeod, Buck and Williams. In these experiments the subject looks at an oscilloscope screen on which dots appear at random with controllable density and frequency of occurrence. They are, however, bright enough and few enough in number for it to be reasonable to assume that retinal factors do not limit their perception. The dots are not placed entirely at random, but some pattern is superimposed, such as an increased density in a particular region. One hopes, with such a stimulus, to break through the retinal barrier and study the ability of central mechanisms to detect these patterns. With suitable arrangements for delivering dots at random or in a controlled pattern, and for counting the numbers that appear, one can apply an absolute statistical measure to the ability of the higher centres to detect the stimulus. This is exactly analogous to Rose’s measure of quantum efficiency, but in this case we aim to be limited, not by the quantum-catching powers of optics, receptors and pigments, but by the pattern-catching powers of the central mechanisms.

Figure 3 shows examples of such random dot patterns. The top left has only the uniform random dot background, while the bottom right has an obviously superthreshold number of extra dots in the centre. The other two are intermediate. Note that we know the external signal/noise ratio of the stimulus for any given average number of dots added to the centre. If we find the internal signal/noise ratio, or \( d' \), the ratio of the two gives a measure of how efficiently one can make discriminations on the basis of the internal representation. Actually, to make it analogous to quantum efficiency, one uses the square of this ratio, and this can be regarded as an estimate of the times when doing frequency of seeing curves without the risk of finding an unresponsive subject asleep on his bite bar.

You do not see such marked habituation effects in ganglion cells, and MacLeod has proved convincingly that they are central; cone stimuli habituate rod-detected flashes, and vice versa, and the effects are size-specific. I expect the habituation is related to the Troxler effect, the disappearance of flicker and also to the fading that occurs in stabilized images. But whatever it is due to, clearly one must take it into account in interpreting data on absolute threshold. Hallett’s calculations also suggest that the instability of the criterion over long periods is important.

The current line of thinking makes one doubt the assumption that the cortex deals efficiently with the evidence provided to it by the sense organs—an assumption that has been implicit in much of the work on the threshold. There is a method whereby this efficiency can be measured and this will now be described.

Estimating Central Efficiency

In these experiments the subject looks at an oscilloscope screen on which dots appear at random with controllable density and frequency of occurrence. They are, however, bright enough and few enough in number for it to be reasonable to assume that retinal factors do not limit their perception. The dots are not placed entirely at random, but some pattern is superimposed, such as an increased density in a particular region. One hopes, with such a stimulus, to break through the retinal barrier and study the ability of central mechanisms to detect these patterns. With suitable arrangements for delivering dots at random or in a controlled pattern, and for counting the numbers that appear, one can apply an absolute statistical measure to the ability of the higher centres to detect the stimulus. This is exactly analogous to Rose’s measure of quantum efficiency, but in this case we aim to be limited, not by the quantum-catching powers of optics, receptors and pigments, but by the pattern-catching powers of the central mechanisms.

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Fig. 3. Eight hundred dots are randomly spread over the whole square, and viewed under conditions where they can readily be seen. A small central square of 1/25 the total area has 32 dots expected, with standard deviation \( \sigma = 5.6 \). \( \Delta N \) dots are added to this central square, the four values corresponding to about 0.4, 8 and 16 times \( \sigma \). From the results plotted in Fig. 4 it will be seen that an excess of 23 dots could be detected with high confidence on about 70% of trials, with some uncertainty in about 95%. Without experience much larger values of \( \Delta N \) are required for confident detection.

This proportion of the sample of dots that is effectively utilized in deciding about the pattern.

Figure 4 shows one method of measuring internal signal/noise ratio, and it is clearly similar to Hecht, Shlaer and Pirenne’s method. There were 800 dots, 32 expected in the central square. One varies the extra dots in the central square and does frequency of seeing curves to which regression lines are fitted. From this the fraction of statistical information utilized is determined. In this case the subject judged “probables” as well as “seen” patterns, and the efficiencies were 39% and 54%.

The figure obtained varies of course with the stimulus parameters, but even after seeking out the optimum it is not easy to better 50%, and at present this seems the most likely way of reconciling the 5.5 quantum efficiency obtained from psychophysics with the 11% lower limit of photometric quantum efficiency.
Conclusion

Psychophysical estimates of “noise” are of the right magnitude to reconcile photometric and behavioural data. But although some noise comes from the retina, and probably the receptors, there is also an important central component. Perhaps after 30 years investigating these central mechanisms we shall understand why they perform as well and as poorly as they do, just as the studies on the receptors that have been presented at this conference are beginning to show what underlies the capacity of a rod to respond to a single quantum, a fact deduced from psychophysical measurement more than 30 years ago.

Acknowledgments

My thanks are due to Dr. A. van Meeteren and Mr. B. Reeves for help in the experiments shown in Figs 4 and 2.

References

9. F. Zwas and M. Alpern 1976, The destiny of human rhodopsin in the rods, Vision Res. 16, 121-128.

Discussion

Gordon L. Fain: Recordings from single rods and cones during light adaptation suggest that the difference in the dark lights of the scotopic and photopic systems may arise, at least in cold-blooded vertebrates, from differences in the photoreceptors themselves. That is, the ratio of dark lights for single rods and cones is nearly as great as that for the scotopic and photopic systems. This finding is of some interest, since it suggests that the difference in the dark lights of the rod and cone systems may be in large part the result of differences in the process of transduction within the two photoreceptor types.

If the difference in the dark lights of the rod and cone systems were due to a difference in the noisiness of the two systems then, at least in cold-blooded vertebrates, one would expect to find the major source of this noise in the photoreceptors themselves. If the noise occurred somewhere within the
process of phototransduction, as for example rhodopsin molecules spontaneously bleaching, then one would expect it to contribute to the voltage noise of the receptors. In fact, the measured noise of receptors gives some credence to this idea, since the magnitude of the noise in rods and cones is nearly the same (see Simon and Lamb, this volume, p. 303) but the sensitivities of rods and cones are different. Thus the number of presumed spontaneous events would have to be much greater in cones than in rods to produce the same amplitude of noise, and this would correspond to the larger dark light in cones.

It is important to realize, however, that the difference in the dark lights of single rods and cones can be explained without any reference to their voltage noises. It is possible to show, for example, that the dark light of a photoreceptor, \( I_0 \), is given by

\[
I_0 = \frac{S^p \Delta V_T}{k},
\]

where \( S^p \) is the sensitivity of the dark-adapted receptor (measured in voltage per incident quantum), \( \Delta V_T \) is the voltage response in the receptor at the behavioural increment-threshold, and \( k \) is the Weber constant of the behavioural increment-threshold curve (see G. L. Fain, this volume, p. 305).

Thus the differences in dark lights between single rods and cones can be explained simply by their different absolute sensitivities and by a difference in the mechanism of light adaptation in the two receptor types. Although rods and cones are both inherently noisy, this noise must be carefully distinguished from the dark light of light adaptation, since these two may be completely different phenomena.

**H. B. Barlow:** We agree with each other that the dark lights of single rods and cones differ approximately as predicted from psychophysics, and I would concede that the relationships can be described as Dr Fain outlines in his last paragraph. But this is not really an explanation, or is very incomplete as such, for it says nothing about why \( k, S^p \), and \( \Delta V_T \) in his expression for the dark light \( I_0 \) have the values they do for rods and cones.

As background illumination is decreased the toad rods and turtle cones both increase in sensitivity, but when the background illumination drops to a value around their respective dark lights the sensitivities reach their plateaus and do not improve any further. One can regard these plateau values of \( S^p \) as the ultimate factors responsible for the difference between rods and cones, as I think Dr Fain does. Alternatively you can take the dark light as more than a mere abstraction and suppose that sensitivity fails to go on improving as real background is decreased because it is the sum (dark light + real light), that controls sensitivity, and this cannot be reduced below the value of the dark light even when real light drops to zero.

My proposal is that the cones in darkness have a much higher on-going signal than rods, possibly because of greatly increased isomerization due to the shift of their peak sensitivity to the red (see Discussion following Simon and Lamb’s paper, this volume, p. 301). This is the intrinsic noise, which I would identify with the dark light \( I_0 \), and threshold signals must be detected as increments to it. On this view both the poor absolute sensitivity of cones, and their high incremental sensitivity (low Weber fraction) relative to rods are explained: cones do not have as high an absolute sensitivity as rods because their intrinsic noise stops them improving their sensitivity as much (if they did have as high sensitivity they would have an absurdly high electrical noise level); and they have better incremental sensitivity than rods because at their absolute threshold they must respond to small changes in the rate of noise events plus photoisomerizations if they are to signal the weakest lights that are statistically significant. This consideration does not apply to rods because the smallest significant number of photoisomerizations is not small compared to the number of noise events.

With regard to light adaptation I agree that the dark light, or equivalent background light, whose slow decline accompanies the slow process of dark adaptation, may best be kept separate from the irreducible dark lights that limit absolute sensitivities. The view that the changes in dark adaptation are paced or controlled by changes in a peripheral source of “equivalent background light” does not now look tenable. However, it may still be the case here again that sensitivity is controlled by a process occurring at a more peripheral point in the chain of transduction than the one at which it is measured.

Finally it is worth saying that human rods may not behave like toad rods, for their electrical response characteristic may not change much until saturation values of the background are reached. Here changes of sensitivity over most of the scotopic range presumably occur more centrally.

**P. B. Fellgett:** I would like to raise the following three points about Dr Barlow’s paper.

1. The term “quantum efficiency” is often used in a loose and poorly defined sense. In relation to the concepts described by Professor Rose (Chapter 1 of this volume), we have to begin with noise-equivalent photon number. This is defined as the minimum number of photons that could in principle enable a particular task to be performed. The ratio of this number to the actual mean number of photons available to a detector by use of which the task can just be performed, is defined as the noise-equivalent quantum efficiency of the detector in that task.
One should consider more precisely the nature of the task in relation to which noise-equivalent quantum efficiency is evaluated. The only safe procedure is to evaluate the information gain in performing the chosen task, since the noise-equivalent quantum number is then precisely fixed. In simple cases, it may indeed be possible to work in terms of signal-to-noise ratio, frequency of seeing etc., but information-theoretic verification is always advisable.

Just because informational estimates are safe they always give a lower limit, and if any part of possible information gain is neglected the noise-equivalent quantum efficiency will be underestimated. This will happen, for example, if we neglect colour information or the ability of the observer to say in which part of the visual field a test flash occurred.

My understanding of the figures that have been presented is that safe estimates of the noise-equivalent quantum efficiency of the eye are about half the supposed quantum efficiency of the primary response to light. Bearing in mind the difficulty of constructing an n-stage image-processing system in which each stage causes a loss of only $2^{1/8}$ on average, it seems to me that so far from there being any "discrepancy" to explain, the human visual apparatus has been extraordinarily well designed and constructed to give so small a ratio between primary and noise-equivalent performance.

H. B. Barlow: Professor Fellgett raised three points which I shall comment on sequentially.

1. Yes, quantum efficiency is used in the following four different ways, at least; (i) the average proportion of quanta entering the eye that is absorbed in receptors, or a particular type of receptor; (ii) as above, but for isomerization or bleaching rather than absorption; (iii) the average proportion of quanta absorbed in a photopigment that cause isomerization or bleaching; (iv) the minimum proportion of quanta entering the eye that would enable the task to be performed. The last is, as Fellgett points out, the "noise equivalent quantum efficiency", and it involves a different principle, for in the first three one is only concerned with the energy of photons, whereas in the fourth one is also concerned with their uncertainty properties. The context usually makes it clear which sense is used and I hope no one was in doubt about my meaning.

2. I do not think Professor Fellgett is right in saying "information gain" is the only safe quantity to evaluate. The important point when calculating noise equivalent photon number is to make sure that one calculates the minimum number of photons for exactly the same task the subject is performing. If the subject is neglecting colour information, or may receive a stimulus in a number of positions but does not have to specify where it occurs, then he is likely to be ignoring some of the information available to him. But this does not invalidate the estimate of noise equivalent quantum efficiency provided that we calculate noise equivalent photon number for the same task as he performs. The value obtained may of course vary with the task, and if it does this is of special interest, for the reasons given below.

3. Yes, the system as a whole is quite efficient at certain tasks, but one cannot know in advance what tasks a biological system is adapted to perform well. It is therefore specially interesting to see what tasks are performed efficiently, what tasks inefficiently. But there is another point. One observer that selective pressure can lead to a reflecting tapetum that causes at most a 50% or so increase in quantal absorption, and must carry the penalty of much greater intraocular scattered light. Consequently one also wants to know about the causes of minor losses of efficiency, because apparent inefficiency may point to important limiting factors that we are not yet aware of.

S. Yeandle: Remarks on the noise of invertebrate photoreceptors. At this meeting we have heard that in dim light the vertebrate photoreceptor develops hyperpolarizing potentials of the order of tens of microvolts per absorbed photon. Furthermore, its intrinsic noise is not small compared to signals generated by single photon absorptions. This seems a strange device to detect dim light. I think it should be pointed out that the arthropod receptor has what appears to be a more reasonable way to detect dim light. Although the essentials of how it does this have been known for some time, I think, for two reasons, it would be worthwhile to review the present knowledge of what occurs in a dark adapted arthropod photoreceptor exposed to dim light. First, it works differently from the vertebrate photoreceptor and, second, it has many features analogous to man-made devices as, for example, photomultipliers.

Briefly, in the dark-adapted arthropod photoreceptor very weak pulses of light evoke a response consisting of a variable number of discrete waves of depolarizing potential, originally called quantum bumps.\(^1\) \(^2\) \(^3\) Available evidence suggests that each photon captured by the visual pigment has a certain probability, \(p\), of triggering a bump. I will confine my remarks to Limulus, the horseshoe crab, because of my familiarity with this creature and because, of all arthropods, most is known about how its photoreceptors react to dim light.

In Limulus one can record intracellularly, from ommatidia in the lateral eye, bumps whose amplitudes can be in the millivolt range. In each ommatidium there are many primary receptors, called retinula cells, which capture photons and one or occasionally two secondary neurones, called eccentric cells, which generate the nerve impulses that travel up the optic nerve.\(^4\) The retinula cells are electrically coupled to each other and to the eccentric cell.\(^5\) \(^6\) When
sufficient bumps occur so that the eccentric cell depolarizes below a threshold level, a nerve impulse is generated.\(^\text{11}\) The number of bumps following a short pulse of light is a random variable with a Poisson distribution whose parameter is proportional to the average energy of the pulse. This finding is consistent with the idea that each photon captured by the visual pigment triggers a bump with probability \(p\).\(^\text{7}\)

One can also record bumps from receptors on the ventral side of the animal called ventral photoreceptors that do not generate nerve impulses and have no known function.\(^\text{8}\) Despite this, the responses to light of the ventral photoreceptor have been extensively studied because its responses are very similar to those of the retinular cell and because its large size and the absence of screening pigments, such as occur in the lateral eye, make many difficult experiments technically feasible. Estimates of \(p\), defined above, for ventral receptor bumps range from 0.02 to 0.5.\(^\text{9}\)

Both the amplitude of bumps and the latency between photon absorption and bump occurrence vary randomly.\(^\text{10, 11}\) The latency ranges from 60 millisecond to over 2 seconds at room temperature, and its probability density function can be fitted by a Gamma function.\(^\text{12}\) The amplitudes, ranging from less than a millivolt to over ten millivolts, appear to be bimodally distributed into large and small bumps. The precise forms of both the amplitude and latency distributions appear to vary from preparation to preparation and the factors responsible for this variability have yet to be worked out. Controversy exists as to whether large bumps and small bumps have different latency distributions.

Extensive studies on the statistics of bump occurrence have led to the following two postulates: First, each absorbed photon has a probability of generating a stochastic process whereby either only one bump is produced at some variable time after the photon absorption, or no bump is produced at all. Second, the stochastic processes initiated by absorbed photons are statistically independent of each other. These two postulates have only been tested for very dim lights, where they seem to hold, but they doubtless fail for sufficiently bright lights. Among other things, they imply the theorem that the distribution of intervals between successive bumps evoked by steady light is a negative exponential whose argument is proportional to light intensity.\(^\text{13}\) This has been observed experimentally in dim lights.\(^\text{7, 14}\) (This theorem, although it seems trivial, is not, and was proved some years after the experimental work on the statistics was done.)

It should be emphasized that the above two postulates are not the only ones consistent with present data. A more precise knowledge of \(p\), the number of bumps per absorbed photon, is at least required before judging if competing statistical hypotheses can be eliminated.

When a receptor is exposed to moderately intense light, the average size of the bumps decreases. This observation has led to the adapting bump model\(^\text{15, 16}\) which postulates that the receptor potential is the summations of quantum bumps whose average size is determined by the degree of adaptation of the receptor. This model has had considerable success in describing the ommatidial potential as recorded intracellularly at the eccentric cell in Limulus.

Bumps occur in the dark and appear to be statistically independent of light evoked bumps. The origin of these so called dark bumps is obscure. In the lateral eye the relationship between rate of occurrence and temperature suggests that dark bumps result from the spontaneous thermal isomerization of visual pigment molecules.\(^\text{17}\) Contrariwise, in the ventral receptor there is evidence that a large proportion of small bumps arise by some process not related to the process producing light evoked bumps.\(^\text{18}\) However, there is some experimental evidence supporting the suggestion that many of the small dark bumps in the ventral receptor may result from the bathing solution used, or injury caused by microelectrode impalement.\(^\text{18, 19}\) The nature of the dark noise in the vertebrate receptor does not appear to be altogether clear but may not arise entirely from spontaneous isomerizations of visual pigment molecules.

To sum up, the occurrence of bumps appears to follow the same laws as the occurrence of shots from the anode of a photomultiplier. Also, as in the photomultiplier, there is considerable gain in the transduction of light. However, bumps differ from photomultiplier shots in two important ways. Bump size is dependent on the past history of illumination and there is wide fluctuation in the time between photon absorption and bump occurrence. In the vertebrate receptor any analogy to a man-made device is difficult to see.

References to discussion comment of S. Yeandle

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