

investigate this possibility. We find that, for vision, slope of the line ΔI against I increases with age, whereas there is no consistent change in the intercept. Some of our results are given in Fig. 1. This suggests that neural noise (m) increases with age, whereas retinal noise (k) does not. It is interesting to consider functional losses associated with ageing as due in part to increase in neural noise. This may be supposed to affect memory storage and recall mechanisms (producing errors or delay) and also motor control, producing tremor and increase in decision or reaction time.

This at least is a crude and inadequate model; in particular, it takes no account of the level of adaptation of the eye.

We wish to acknowledge help given, at various times, by members of the Nuffield Unit for Research on Ageing, particularly Dr. J. Szafran, and also by R. T. Leslie, E. R. F. W. Crossman, A. Kendon and Miss J. Wallace, who is in receipt of a grant from the Medical Research Council, which has also made us a grant for apparatus.

VIOLET CANE

Department of Mathematics,
Queen Mary College,
London, E.1.

R. L. GREGORY

Psychological Laboratory,
Downing Place,
Cambridge.

BOTH Bulmer and Howarth and Cane and Gregory accept the logarithmic relation between impulse frequency (r) and light intensity (I) expressed in the formula $r = \eta + b \log(aI + \epsilon)$ (a , b , constants; η , ϵ , random variables representing neural and retinal noise), but it does not appear to be generally true in the vertebrate retina. Hartline¹ showed that it was approximately true for the compound eye of *Limulus*, and also, under more restricted conditions, in the frog². These results were avidly absorbed by psychologists, because they fitted so well the logarithmic relation between sensation-level and stimulus intensity which Fechner derived by integration of the Weber law; but the maintained discharge of retinal ganglion cells in the cat does not show any such simple relation³, and FitzHugh's results⁴ suggest an almost linear relation between the number of extra impulses evoked and the quantity of light delivered in near-threshold flashes superimposed on a steady background. There may be other types of ganglion cell, not readily isolated by present techniques, which behave in a different way, but it seems rash to use the logarithmic relation in formulating a theory of visual noise.

There are two further criticisms of the formulation which Cane and Gregory now put forward. First, it fails to recognize that the variance of ϵ (the retinal noise which, they say, includes quantum fluctuations) must increase when I is increased. Second, so many hypothetical quantities (m , k , η , ϵ , c , a , b , and V) are introduced that it would be a formidable, or impossible, task to evaluate them experimentally. The complications introduced by considering a second source of noise do not seem justified until facts are found which cannot be explained by a simpler theory.

These difficulties can be avoided if one does not express noise as variance of impulse frequency. There are other possible units of measurement which can be defined as precisely, which are more easily derived from measurements of visual performance,

and which may be more simply related to the cause of noise. In one of the papers⁵ which Bulmer and Howarth discuss, the natural unit arising from the method is the average number (x) of random independent events (such as the spontaneous activation of a rod) which are liable to be confused with the absorption of a quantum of light: the maximum value of x was shown to be related to the number of quanta absorbed from threshold flashes and to the slope of frequency-of-seeing curves. Recently Rushton⁶ estimated that 1/10 of the quanta (507 m μ) incident at the pupil are absorbed in the rods; using this figure, and previous results on absolute threshold, the method shows that x cannot exceed 10.

One might hope to compare this figure with estimates of noise obtained by different methods, and this can be done, though the comparison is not at all exact. If plausible assumptions are made⁷ about the area and time within which stimulus and noise events are liable to be confused, one can calculate the intensity of a steady light which would lead to the absorption of 10 quanta, on the average, in such an area and time. This light would send about 1,000 quanta/sec. deg.² into the eye, and it can be looked upon as a 'dark light' which causes noise at the absolute threshold. It should have the same value as the *Augenschwarz* of Fechner⁸, the *Eigenlicht* of Helmholtz⁹, and Gregory and Cane's¹⁰ k , or k/a . It is, in fact, lower than any of them, but measurements of the difference threshold similar to those upon which the above quantities were based have been made^{7,11} under conditions where rods alone are active, and these yield values for the dark light which fall in the range 200–3,000 quanta (507 m μ)/sec. deg.² entering the eye. It can also be shown that the mean and the variance of frequency of the maintained discharge of ganglion cells of the cat's retina are probably compatible with such a dark light, though, as Bulmer and Howarth point out, there are difficulties in relating the two.

These three otherwise unrelated results could all be explained by a dark light of the order of magnitude of 1,000 quanta (507 m μ)/sec. deg.², and this approximate agreement provides some experimental justification for the concept of retinal noise. Furthermore, if a large part of it is caused by thermal decomposition of photosensitive pigments, one can relate the higher dark light and reduced sensitivity of cones to the shift to the red of their spectral sensitivity curves¹². Thus the difficulties raised by Bulmer and Howarth, and the complexity which Gregory and Cane's formulation requires, are avoided if visual noise is measured as dark light, not as variance of impulse frequency. There will, however, be plenty of room for argument until the source, or sources, of visual noise are known with greater certainty.

H. B. BARLOW

King's College, Cambridge.

¹ Hartline, H. K., *J. Cell. Comp. Physiol.*, **1**, 277 (1932).

² Hartline, H. K., *Amer. J. Physiol.*, **121**, 400 (1933).

³ Kuffler, S. W., FitzHugh, R., and Barlow, H. B., *J. Gen. Physiol.*, **40**, 633 (1957).

⁴ FitzHugh, R., *J. Gen. Physiol.* (in the press).

⁵ Barlow, H. B., *J. Opt. Soc. Amer.*, **46**, 634 (1956).

⁶ Rushton, W. A. H., *J. Physiol.*, **134**, 30 (1956).

⁷ Barlow, H. B., *J. Physiol.*, **136**, 469 (1957).

⁸ Fechner, G. T., "Elemente der Psychophysik" (Breitkopf und Hartel, Leipzig, 1860).

⁹ Helmholtz, H. von, "Handbuch der Physiologischen Optik", II Auflage (Hamburg und Leipzig, 1896).

¹⁰ Gregory, R. L., and Cane, V., *Nature*, **176**, 1272 (1955).

¹¹ Aguilar, M., and Stiles, W. S., *Optica Acta*, **1**, 59 (1954).

¹² Barlow, H. B., *Nature*, **179**, 255 (1957).