

corresponding roughly to 80, 50 and 20 per cent positives.

Assuming that  $r \propto \log(I + k)$ , where  $k$  is a positive constant, possibly related to the noise background, the authors deduce the equation:

$$1 + \frac{\Delta I}{k} = \exp(C + \alpha\sqrt{I/A}) \quad (2)$$

for the absolute threshold  $\Delta I$  for an area  $A$ . In this equation the constant  $\alpha$  is a positive multiple of  $\beta$ , the constant on the right of equation (1).

The authors proceed to derive Ricco's law for small fields and Piper's law for larger fields from equation (2). But their derivations involve implicitly the assumption that  $\alpha$  is positive; this is true when the threshold is defined by 80 per cent positive responses, but for about 50 per cent positive responses  $\alpha$  is zero, and for lower values it becomes negative.

Equation (2), in fact, implies that for some definition of threshold for which  $\alpha = 0$  (about 50 per cent positive responses),  $\Delta I$ , the absolute threshold in terms of illumination, is independent of area. The variations with area for other definitions of the threshold are due to the frequency of seeing curves plotted against  $\Delta I$  for large areas being steeper than those for small. For 80 per cent positive responses  $\Delta I$  increases as the area diminishes, as the authors conclude; but for 20 per cent positive responses,  $\Delta I$  diminishes as the area diminishes, becoming negative for very small areas.

The fallacy lies in deriving an equation for the threshold applicable only to the particular areas  $A_1$  and  $A_2$  considered, and then varying the areas without considering which of the other quantities in the equation remain invariant under this treatment. In equation (1),  $C$  is defined for the areas  $A_1$  and  $A_2$ ; there is no reason for supposing that in equation (2)  $C$  will remain constant while  $A$  is varied. Further, the relationship  $r \propto \log(I + k)$  is certainly not true for small areas if the area is varied. Hartline's<sup>3,4</sup> experiments showed that in the eye of the frog over a wide range of intensities and areas  $r$  depends on the total flux  $IA$ . The human retina is also composed of a mosaic of functional units, and there is every reason for believing that in the present respect these units behave like the functional units of the frog. Further, diffraction and optical defects may make the images of very small areas virtually identical. These facts provide the simple and generally accepted explanation of Ricco's law—and certainly a theory which seeks to explain the law without taking them into consideration must be regarded with the gravest suspicion.

The authors' assumptions thus do not lead to reasonable conclusions about visual thresholds, and considerable modifications to their theory are required before it can be regarded as a useful approach to the problems of visual excitation.

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<sup>1</sup> Gregory, R. L., and Cane, V., *Nature*, **176**, 1272 (1955).

<sup>2</sup> Cane, V., *J. Roy. Statist. Soc.*, **B**, **18**, 177 (1956).

<sup>3</sup> Hartline, H. K., *Amer. J. Physiol.*, **130**, 690 (1940).

<sup>4</sup> Hartline, H. K., *Amer. J. Physiol.*, **130**, 700 (1940).

IN our first communication<sup>1</sup> on this subject we did not consider the effect of changing shape of the distribution of the neural impulse-rate,  $r$ , with consequent change in variance, as the photic intensity,  $I$ , decreases.

We have, however, considered this in later papers<sup>2,3</sup>. Marriott's prediction from our original formulation that  $\Delta I$  would become negative for stimulus conditions giving a sufficiently small percentage of positive responses depends on the distribution being normal. It is quite clear, however, that the distribution must change at low intensities, for a negative pulse-rate is impossible, and so it must become asymmetrical for low values of  $r$ . Now when we consider threshold conditions for various areas of stimulation, the pulse-rate for a given fibre must rise as the area,  $A$ , is reduced, if the threshold is to be maintained. But since fewer fibres are stimulated, the total number of impulses in unit time might not rise. We are inclined to think that for human central vision, at least, detection is based on the average pulse-rate. One of our reasons for holding this view is that in detecting a signal,  $\Delta I$ , against a background,  $I$ , increases in the area of the background produce a lower threshold for discriminating the  $\Delta I$  field<sup>4</sup>. It should be noted that this result does not hold for short flashes of  $\Delta I$ . In this case (and most threshold determinations are made using short flashes) the background area has no effect, suggesting that the discrimination for short flashes of the signal, as opposed to continuous viewing, is a matter of detecting changes over time rather than over space. The experimental finding, that increase in background area, for continuous viewing, produces a reduction in the signal intensity ( $\Delta I$ ) required, suggests to us that no mechanism such as retinal facilitation will account for areal summation. It looks as though perception involves selecting relevant areas in the stimulus field. For example, if a narrow black ring is added to the background in the differential threshold situation, so that the signal lies at its centre, the threshold rises, and is the same as though the part of the background lying outside the ring were not there<sup>4,5</sup>.

A further reason for thinking that average pulse-rates are used is that, for intensities well above absolute threshold, a larger area does not appear brighter than a smaller one of the same intensity, as would be expected if the total pulse-rate were being used as criterion. It is also the case that objects do not appear brighter when viewed with both eyes rather than one, though the threshold falls.

Although we would defend our general approach, there is the difficulty, pointed out by Dr. Marriott, that the threshold should not change when it is determined by 50 per cent positive responses. We do not ourselves know what the result for thresholds defined by 50 per cent or fewer correct responses would be, using the frequency-of-seeing method. Other methods produce a positive bias at low intensities, because there are fewer possible readings below the 50 per cent point than above it. Published frequency-of-seeing curves relate to flashes and do not give the information required.

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<sup>1</sup> Gregory, R. L., and Cane, V. R., *Nature*, **176**, 1272 (1955).

<sup>2</sup> Cane, V. R., *J. Roy. Statist. Soc.*, **B**, **18**, 177 (1956).

<sup>3</sup> Cane, V. R., and Gregory, R. L., *Nature*, **180**, 1403 (1957).

<sup>4</sup> Gregory, R. L., *Information Theory*, Third London Symposium (Butterworths, 1956).

<sup>5</sup> Fry, G. A., and Bartley, S. H., *Amer. J. Physiol.*, **112**, 414 (1935).