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THE SIZE OF ROD SIGNALS

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SUMMARY

1. This investigation is based upon Alpern's (1965) contrast flash observations. The threshold for the test flash λ (Fig. 2*a*) is raised if a second flash ϕ falls on the annular surround. Moreover, if λ excites rods at threshold, it is only the rods in the surround that contribute to the threshold rise.

2. The possibility that the rise in λ threshold might be due to light physically scattered from surround to centre we exclude by several different experiments. We conclude (Fig. 1*b*) that the ϕ flash sets up a nerve signal N which is conducted to some place C where it inhibits the signal from the centre.

3. If the luminous surround, instead of being a full circle (Fig. 2*a*) consists only of the sectors shown black in Fig. 2*b*, that occupy $1/m$ of the surround area, it is found (in the physiological range) that the light/area on those sectors must be m times as great to produce the same threshold rise at centre, i.e. the total surround illumination must remain the same.

4. This result would obviously follow if N, the inhibitory nerve signal, were proportional to the total surround illumination. We have established the converse; the signal *must* be proportional to the quantum catch.

5. Light can be increased indefinitely, nerve signals cannot. When ϕ increases sufficiently, N saturates in the same way that S-potentials and receptor potentials saturate, namely according to $N = \phi/(\phi+\sigma)$ where σ, the semi-saturation constant is about 200 td sec, or 800 quanta absorbed per rod per flash.

6. Thus the nerve signal N is proportional to the quantum catch over 4 log units in the physiological range, namely from 1 quantum per 100

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rods to 100 quanta per rod per flash. Above this for another 2 log units N continues to increase, but now more slowly, after the manner of S-potentials and receptor potentials.

INTRODUCTION

The size of rod signals

It is generally agreed that a rod can be excited by the catch of a single quantum (Hecht, Shlaer & Pirenne, 1942) and that rod signals converge upon some 'summation pool' which responds to the total flux of signals, more or less independent of the particular rods excited. This may be

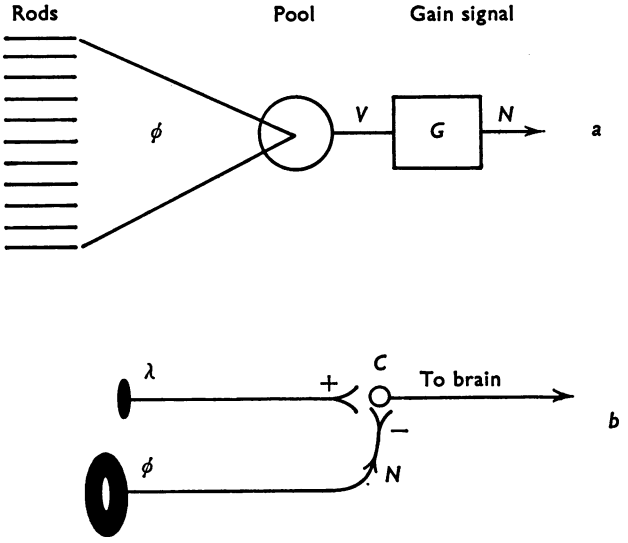

Fig. 1. (*a*) Scheme showing the effect of a flash of light ϕ. The pooled rod response V is modified by a variable gain box G to produce the output N. (*b*) Alpern & Rushton (1967) model (simplified) to explain contrast flash interaction. The surround flash ϕ produces a response N which inhibits at location C the response produced by the test flash λ. For λ to be detected its intensity must be increased compared with the value required in the absence of ϕ.

diagrammatically indicated by Fig. 1*a* (where nothing except rods represents any special histological structure). The size or efficacy of the pooled signals, V, is modified by a variable gain box, G, which is affected by adaptation, as will be considered in the following paper. Here we are simply concerned to know the size of the rod signal, V, set up in the 'summation pool' of the dark adapted human retina by 100 msec flashes of various energies.

What we observe is a set of psychophysical thresholds from which something definite and surprising may be inferred, namely that nerve signals increase in direct proportion to the rod quantum catch over a range of about 4 log units. Above this, saturation sets in. A retinal illumination of 1 scotopic td results in the catch of about 4 quanta per rod per second (Denton & Pirenne, 1954; Rushton, 1965). The strongest flashes we use are about 6 log td lasting about 100 msec which involve the catch of some 400,000 quanta per rod per flash. We claim to show that the rod output is proportional to the catch up to 300 quanta caught per rod per flash.

Principle of the analysis

Electrical measurements such as *S*-potentials, e.r.g., etc., vary in magnitude with light energy. Compared to these the psychophysical threshold is limited, for it is restricted to the lowest point of a range of brightness values, and in our conditions of dark adaptation the ordinary threshold is reduced to a single measurement. We cannot explore far in a space of zero dimensions. For our analysis we need manoeuvring room, a space within which we can spin a logical net. In this paper we shall use two dimensions, gaining one by using not the simple visual threshold, but the contrast-flash threshold of Alpern (1965) and Alpern & Rushton (1967).

Contrast flashes

Two flashes are applied as shown in Fig. 2*a* the test flash λ upon a 2° central circular patch, and nearly simultaneously a much stronger contrast flash ϕ upon a concentric surround annulus of 8° with a 2° black centre. It was found (Alpern, 1965) that ϕ inhibited λ, so that the stronger ϕ was made, the stronger had λ to be if it was to remain still just detectable. It was proved that when the λ threshold is derived from rods, the ϕ inhibitory signal is also derived exclusively from rods. For, by changing the wave-length of ϕ, the energy has to be changed in accord with the rhodopsin action spectrum in order to have the same inhibitory effect. Thus it is only quanta absorbed by *rods* in the surround that inhibit the rod activity at the centre.

This receptor specificity is analogous to Stiles's observations that rod thresholds are raised only by the rods in the background upon which (in his experiments) the test flash falls. Could it be that the Alpern contrast inhibition is nothing more than an undetected Stiles background effect? If some of Alpern's surround light was scattered to the centre and absorbed by rods there, it would form a background to raise the threshold according to Weber–Fechner principles. This, however, is not the way of it.

A strong bleaching light applied to the surround area will desensitize

the rod mechanism there but have no effect upon the scattering of light. Thus if the contrast flash acts by scattering, it will act as strongly after bleaching as before. But if it acts through inhibitory signals arising from the ϕ-rods, now desensitized by bleaching, the inhibition will fail. In fact the inhibition fails and in a most telling quantitative manner. For, to restore the inhibition to its former strength, the ϕ flash needs an increase in precisely the same proportion as does the threshold for seeing the ϕ

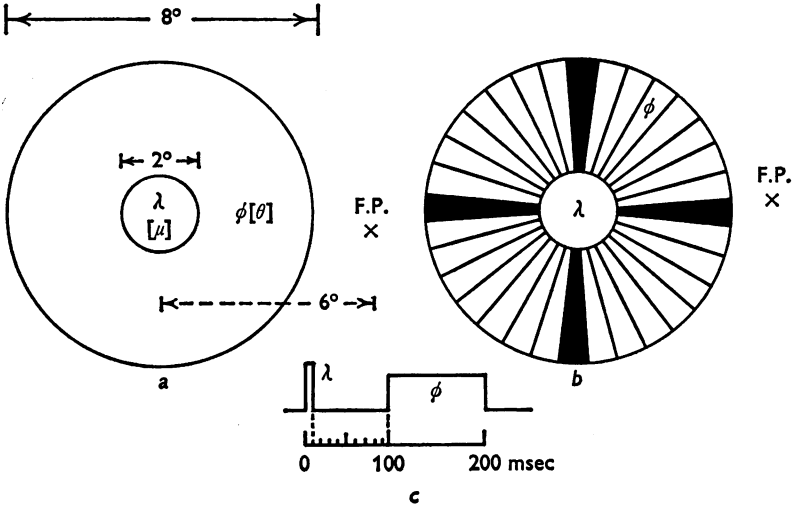

Fig. 2. (*a*) Spatial relations of contrast flashes, (*c*) temporal relations. The ϕ flash falls on an annular region with black centre which just contains the λ flash. This falls 6° from the fovea on the side remote from the optic disk. (*b*) The 'windmill stop' blacks out all but four of the thirty-two sectors, so the surround consists only of the four bright sails here represented black. F.P., fixation point.

flash itself after bleaching (Alpern & Rushton, 1967). That is, log desensitization as measured by the ordinary dark adaptation curve is also the log desensitization of surround inhibition, very strong evidence that rod signals, not light scatter, is what is involved. It is clear, therefore, that the signals λ from the centre are inhibited by the much stronger signals ϕ arising from the surround, and we are led to the schematic representation of Fig. 1*b*.

Signals from λ are inhibited by signals from ϕ, and the greater λ the greater must be ϕ to restore the test flash to threshold. The relation is monotonic (Alpern, 1965, Fig. 4; see also Fig. 4 of the present paper); hence for each value of λ there is one corresponding value of ϕ. Consequently in our study of the relation of the energy of the flash ϕ to the size of inhibitory nerve signals N generated, we have acquired one dimension

of flexibility. By varying λ we vary the threshold ϕ and the size of N. But we need a second dimension before we can manoeuvre sufficiently to eliminate λ and relate ϕ to N directly.

The windmill surround

A new variable is provided by presenting the surround flash (ϕ) not only as the full 360° annulus of Fig. 2*a* but also as a 'windmill' with four luminous sails (shown black in Fig. 2*b*), each occupying $\frac{1}{8}$ of 90°, the other $\frac{7}{8}$ being dark.

The full surround 2*a* may be thought of as consisting of thirty-two sectors each of the size of one windmill sail. Their total inhibitory effect on λ at the centre is thirty-two times the effect of one sector; similarly with 2*b* the effect on λ will be four times the effect of one sector. Thus with the same luminance on all the sectors in Fig. 2*a* and *b*, the inhibitory nerve signal N_a will be eight times N_b. This result ignores the second order effect of mutual inhibition between neighbouring sectors; we give later evidence to justify this simplification.

If we accept that $N_a = 8N_b$ we have now logical space enough to find in principle the relation between ϕ_a the flash energy and $N_a = f(\phi_a)$ the resulting signal. For if we adjust the energies ϕ_a, ϕ_b to give the same λ inhibition, we have

$$f(\phi_a) = N_a = N_b = \tfrac{1}{8}f(\phi_b). \qquad (1)$$

We need not deal with the general problem of extracting the function f given the set of corresponding numbers ϕ_a and ϕ_b, since our actual problem is extremely simple, but to show the power of this type of analysis we use it to disprove (what has often been proposed) that our nerve signal is a logarithmic function of the light energy.

If $$N = c\log\phi,$$

then eqn. (1) becomes

$$c\log\phi_a = \tfrac{1}{8}c\log\phi_b,$$

therefore $$\phi_b = (\phi_a)^8$$

a result that is utterly contradicted by experiment. For it is the light energies, not their logarithms, which in fact stand in a fixed eightfold ratio.

METHODS

The optical arrangement is shown in Fig. 3, designed to present steady background fields μ, θ in addition to the brief flashes λ, ϕ used in this paper. Figure 2*a* indicates (in square brackets) that μ concides in space with λ; θ with ϕ. In Fig. 3 the light source *B* is a straight vertical tungsten coil filament automobile headlamp. It provides four separate channels, the ϕ, θ, μ and λ fields, respectively. The path lengths, and indeed the essential optical components of these four channels are

nearly identical except that the ϕ and λ fields can be flashed each with a pair (one for *on*, and the other for *off*) of Ledex rotary solenoid shutters, *Sh*. The μ and the λ fields are brought together by the mixing cube C_1 and their mutual field stop, s_1, provides the central 2° circular field. The λ, but not the μ, field has a thin wire stretched across its horizontal diameter just before this mixing cube so that the test flash appears as a 2° circle with a thin horizontal black line across it. The θ and the ϕ fields are brought together by the beam mixer C_2 and their mutual field stop s_2 provides an 8° annular surround with a central 2° opaque circular area where the test flash appears. The blacked out area in the s_2 stop was just slightly larger than, though concentric with, the circumference of the inner edge of the s_1 stop. Additional field stops (not shown) could be added say to the ϕ field just behind the mixing cube C_2, for example, to obtain the windmill shown in Fig. 2*b*. The unified ϕ–θ beam and the unified μ–λ beam were brought together by the mixing cube C_3 and the ensemble was seen in Maxwellian view provided by L_3, a type I Kodak Ektar lens, f/2·5, 155 mm focal length.

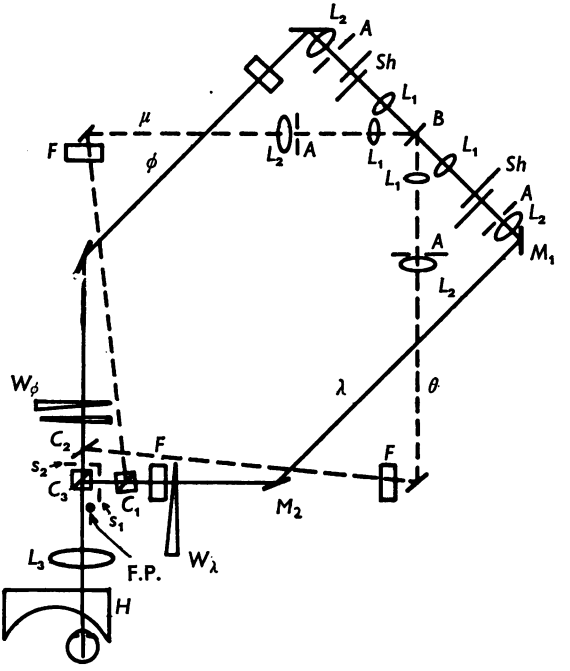

Fig. 3. Plan view of the optical components of the apparatus. The observer's right eye is at the lower left corner within the screening hood, *H*. For details, see text.

Each of the four channels has a lens L_1 (18 mm focal length) which images the filament on the aperture stop A which in turn is imaged by the Maxwellian lens L_3 in the plane of the pupil, all four aperture stops being brought into coincidence there. Immediately behind stop A in each path was the field lens L_2 (172 mm focal length) which images the uniformly illuminated L_1 onto L_3 and hence secures uniform fields. All the beams are deflected as shown by first surface mirrors and modified by coloured and neutral (Wratten no. 96) filters, F. The ϕ beam was also

attenuated by the compensated neutral wedge W_ϕ, and the λ beam by W_λ, uncompensated since the λ area is too small to demand it.

The aperture stop A in the λ field consisted of two 5 mm circular holes one above the other, one filled by the top the other by the bottom of the filament image. These, projected upon the pupil plane, formed two small spots one coinciding with the three other aperture images and the other lying some 3 mm below. The subject's head was fixed so that the coincident beams entered through the centre of his dilated pupil and the second λ spot entered just clear of the lower edge. In this way by occluding one or other of the λ aperture holes, the λ test flash could be sent through centre or periphery of the pupil to confirm (by the absence of Stiles–Crawford effect) that the test did indeed excite rods at threshold, the essential condition upon which the whole of our analysis depends. On account of the eye's spherical aberration, a shift in the point of pupil entry will in general cause a small displacement of the retinal image. Thus if both of the two λ aperture stops are open, in general two non-coincident λ areas (Fig. 2*a*) will be seen. Now the λ area is the image of the field stop s_1 and by suitably adjusting the distance of this stop the two images may be brought into coincidence. This is the position of s_1 used in our experiments.

All of the optical components (lenses, mirrors, filters, shutters and stops) were mounted on standard optical bench saddles rigidly fixed to one of four triangular rails and they in turn were screwed to the table top. This allowed the maximum flexibility in changing field stops, and mixing cubes when necessary from one experiment to the next, or indeed within the same experiment, without disturbing the optical alignment.

The timing of the two rotary switches which provided the *on* and the *off* of flash λ (likewise flash ϕ) was provided by Tektronix pulse generators which triggered the transistors controlling the solenoid currents. The subject pressed a microswitch to initiate the cycle; test and contrast flash followed in a set time sequence. Fig. 2*c* show the sequence generally used, which was monitored by phototransistors and displayed by cathode rays.

RESULTS

The main experiment

The subject (who was usually M.A. or S.T.) had his pupil dilated (mydriocyl or cyclogel) and was properly aligned with a bite board and viewing hood (H, Fig. 3) that fitted the face and excluded most light except through one eye hole. He was left to become dark adapted. Then a series of surround flashes were presented starting at the lowest values to preserve the dark-adapted state. For each ϕ flash the test flash λ was adjusted in intensity by the subject (wedge and filters) so that the horizontal black line on the λ field could just be detected. The background had the 'windmill' stop interposed for alternate settings so that curves A and B in Fig. 4*a* were determined at a single long run. At the highest light levels short periods for dark adaptation were interposed between the threshold exposures.

In the curves of Fig. 4*a* the white circles (curve A) plot log λ thresholds when the full 360° surround was used, black circles (curve B) when the 'windmill' stop was introduced. It is seen, as would be expected, that

curve B lies to the right of A and below it since with the windmill stop the inhibitory signal N is reduced to $\frac{1}{8}$ and thus ϕ must be increased to generate the same inhibition.

Figure 4*a* plots log ϕ against log λ, the test flash intensity, for conditions A and B, but what we need is to combine these to give us Fig. 4*b*, the plot of log ϕ against log N the signal intensity. This may be done as follows. Draw on Fig. 4*a* the irregular flight of stairs shown, which is constructed

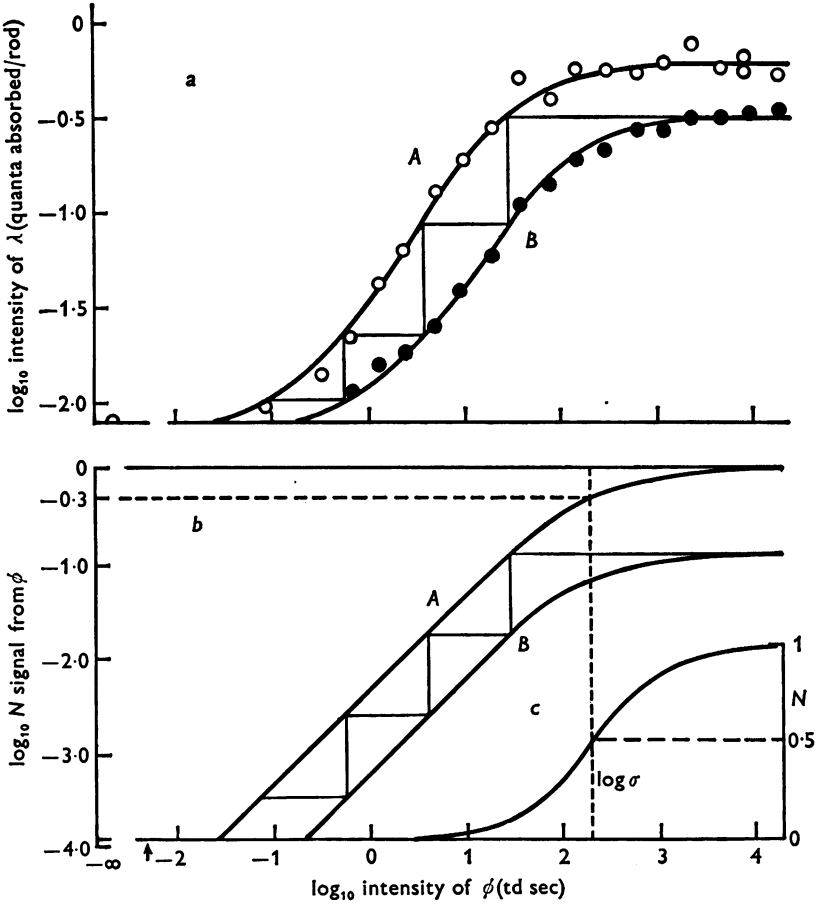

Fig. 4*a*. Results of the main experiment, white circles with full surround ϕ (Fig. 2*a*), black circles with windmill ϕ (Fig. 2*b*). The results are the mean of five successive measurements in a single experimental session for subject S.T. The λ flash wa sblue (Ilford 622 filter), the ϕ flash red (Schott Jena RG 2 glass filter). (*b*) Transformation of the curves in Fig. 4*a* by making each vertical riser of its staircase 0·9 log unit high while keeping the horizontal 'treads' unchanged. This plots log N, the nerve signal. (*c*) Replot of Fig. 4*b* with N instead of log N as ordinate (scale on right).

by starting at any point on A and moving horizontally to the right to meet B, then moving vertically to meet A, and then horizontally to B and so on. The horizontal treads of this staircase measure the increase in log ϕ in going from the circular to the windmill background when λ remains constant, i.e. when the inhibitory signal N remains constant. Consequently, in constructing the log N staircase of Fig. 4*b* we know that in going between these same log ϕ values, the log N remains constant. Thus each horizontal tread is to be brought vertically downward by some amount from the upper staircase to the lower. But the vertical risers of the old stairs, unequal in their effect upon the λ threshold, must all be equal in their effect upon log N since each corresponds to the change from $\frac{1}{8}$ to full circle and hence to an increase of eight times N or 0·9 in the height of log N. Consequently our new staircase Fig. 4*b* is derived from the old one by keeping the treads the same and making each riser exactly 0·9 high.

This transformation reveals something very remarkable. Except at the top, the new staircase is quite uniform and rises at 45°. This is a fact that we have verified over and over again, for it does not require the whole exacting experiment of Fig. 4 but may quickly be confirmed piece-meal. At any level except right at the top, the introduction of the windmill stop together with the removal of a 0·9 neutral filter in the beam is found to have no net effect upon the λ threshold. This signifies that over all that 45° range of staircase, the inhibitory rod signal N is directly proportional to the energy of the light flash, a range of over 3 log units.

Scattered light

Near the outset of this paper we gave good evidence that the contrast flash acts by lateral inhibition rather than by light scatter. Now from the main experiment we have concluded that the inhibitory signal is proportional to the total light flux no matter how that was distributed (radially) over an enormous energy range. This does not accord at all well with our preconceptions about inhibition, but it accords exactly with our views on light scatter. In this and the following papers we build a substantial structure upon the belief that we measure N, the inhibitory nerve signal. It will collapse if the basis is simply scattered light. We have therefore excluded this possibility in a number of different ways.

(i) The method of bleaching the surround has been mentioned earlier. A much fuller analysis of bleaching upon N the inhibitory signals will be given in a later paper. The results are utterly incompatible with the scattered light explanation.

(ii) The amount of light actually scattered from the surround (where the ϕ flash fell) onto the centre (where the λ flash fell) was measured by the method of Rushton & Gubisch (1966). In terms of Fig. 2*a* what they

did was to find by how much the test threshold λ at the centre was raised by steady light either applied directly there (μ) or to the surround (θ). When μ and θ were adjusted to give an equal rise of λ, the ratio μ/θ was found to be constant, independent of actual background intensity i.e. just as though θ acted simply through the constant fraction of its light which is scattered onto the μ area. To show that this was indeed the true explanation they chose an intensity of μ sufficiently strong to bleach the visual pigment to an equilibrium value of about 50 %. Then, changing from this μ to the θ that raised λ equally, it was found that θ also bleached the pigment at centre to precisely that same equilibrium level. Thus when μ and θ raise λ equally they bleach equally and the receptors catch quanta equally from direct μ and from scattered θ. Consequently we may use the μ, θ equivalence for λ to measure the relevant θ scatter.

To facilitate the μ/θ comparison we used only the ϕ path (Fig. 3) keeping the shutter open to give steady light and changing the presentation from centre to surround by changing the field stop from that in the μ beam to that in the θ beam. But the 2° λ *flash* was made slightly smaller so that the increment thresholds were not contaminated with edge effects resulting from small eye movements.

The results of one experiment are shown in Fig. 5*a* where white circles show the threshold rise produced by steady μ backgrounds, black circles by the same steady lights falling now on the θ background. The two curves are separated by 1·1 log units, thus about 8 % of the light falling on the surround is effectively scattered to the centre. Of this we found 3 % to be scattered in the apparatus, thus presumably 5 % was scattered entoptically. How far will 8 % of scattered light account for the rise of λ threshold in Fig. 4 that we have attributed to inhibitory nerve animals arising from the ϕ area?

Figure 5*b* shows an experiment which differs from that of Fig. 5*a* only in that instead of using steady backgrounds μ, θ the backgrounds were presented as 100 msec flashes sent in 100 msec after flash λ (the temporal arrangement of Fig. 2*c* and of the main experiment). The effect of this after-background applied directly to the centre is shown by the white circles of Fig. 5*b*, and we know what to expect of similar flashes applied to the surround *if only scatter operates*. For the fraction of light scattered does not depend upon the duration of the flash, and from Fig. 5*a* we know what it is and may say with confidence, 'The θ-flash and the μ-flash will raise the λ threshold equally if θ is made 1·1 log units stronger than μ, and if physical scatter alone raises the λ threshold.' So we expect the surround flashes ϕ to lie on curve B drawn 1·1 log units to the right of A which is drawn through the white circles. The black experimental points, however, not only do not fall on B, they fall nearly as far from A in the opposite

direction. There are about 2 log units between the black points and curve B, thus the surround flash, as used in the experiments of Fig. 4 raises the λ threshold by a factor which is different from scattered light and 100 times

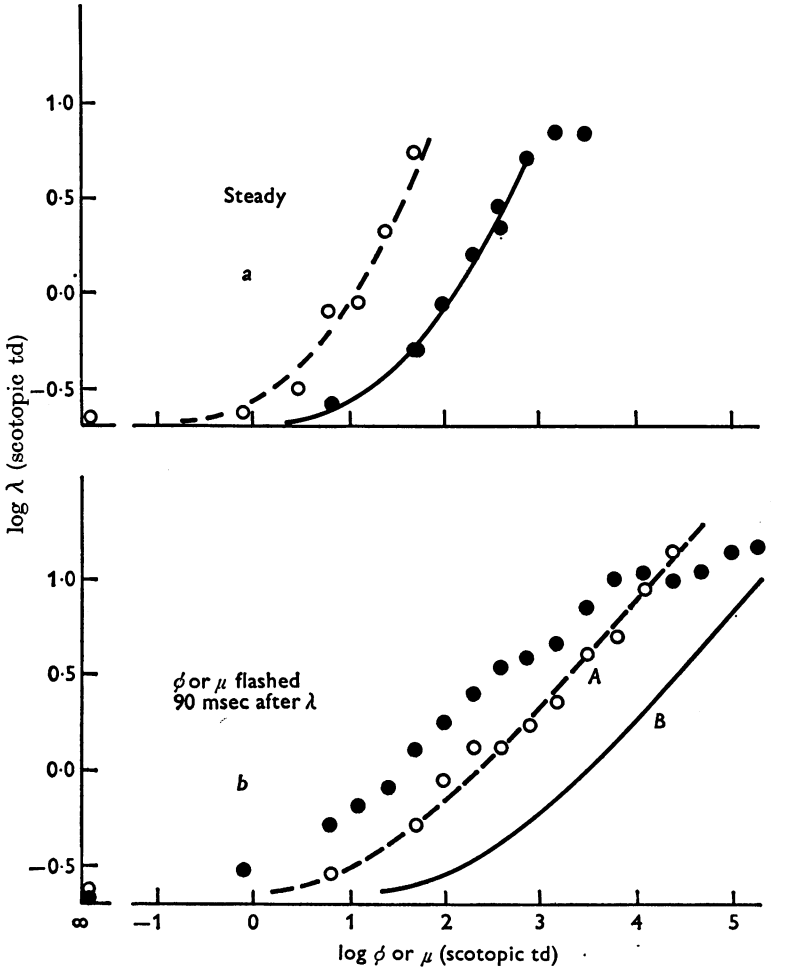

Fig. 5. The effect of ϕ surround (black circles) and μ background (white circles) on the threshold intensity for seeing λ as a function of ϕ (or μ) intensity. In (*a*) the surround or background was steady. In (*b*) it was flashed as in Fig. 2*c*. λ was flashed for 10 msec in each case.

as effective. This is the factor which is reduced by rhodopsin bleaching inversely as the rise in visual threshold. We call it an inhibitory nerve signal, N.

(iii) In estimating the contribution of scattered light to the rise of λ threshold, we cannot diminish stray light, but it is easy to increase it. In

the experiment of Fig. 6 we more than doubled the amount of ϕ flash that falls on the λ area by removing the 2° black patch in the centre of the ϕ field stop (the patch which prevented ϕ from falling directly upon the λ area) and replacing it with a 2° patch cut from a 1·0 density gelatin film. The λ area which formerly received 8% of the ϕ flash by scatter now receives a further 10% through the patch, more than doubling the scatter effect.

The circles of Fig. 6 are just a repetition of the experiment of Fig. 4*a* that plots log λ against log ϕ with the black patch in the centre of the ϕ field stop. The squares (Fig. 6) show the results when black patch was

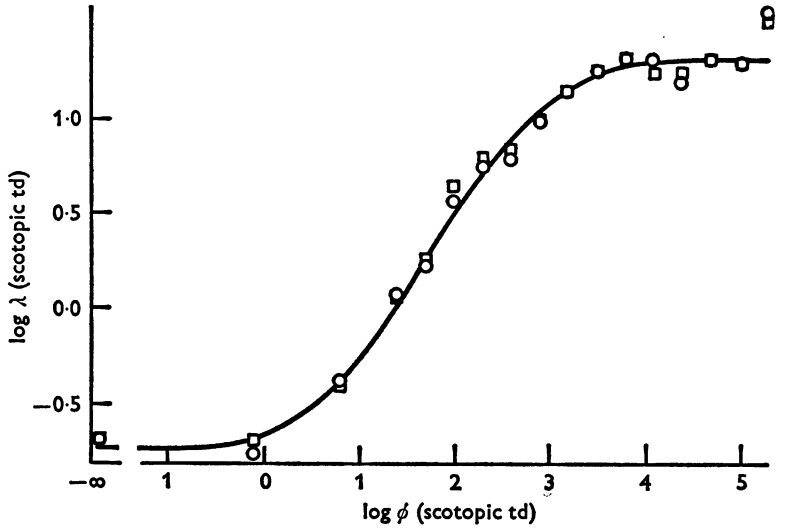

Fig. 6. Effect on the threshold for seeing λ of doubling the light scattered from surround to centre. Circles, when ϕ field is blacked out at centre (as usual), squares, when the black disk is replaced by a gelatin disk of density 1·0.

replaced by the 1·0 density patch, and the scatter more than doubled. The small difference between circles and squares in Fig. 6 shows again that light scatter plays an insignificant part in the influence of ϕ upon λ. This influence is not scatter but a nerve inhibition whose size is proportional to the number of quanta absorbed over a great range. The conclusion is surprising but seems inescapable.

Cone involvement

We never found any contradiction to Alpern's (1965) and Alpern & Rushton's (1965) observations that whatever receptors are excited by λ at threshold, it is only those receptors in the surround that inhibit them. Our

contrast flash was usually red since this strongly excited cones (in addition to rods) and thus, by inhibiting cones in the central test region, increased the range over which λ could excite rods before attaining cone threshold.

We satisfied ourselves that rods and not cones were in fact being excited at threshold by two tests.

(*a*) The test flash λ was arranged so that it could enter the eye either through the centre or the periphery of the dilated pupil. The threshold was usually found to be the same in both conditions. When this was not so it signified that the Stiles–Crawford effect was in operation. Since this only applies to cones and always applies to cones, results showing the effect were rejected; the threshold of those remaining must be rods and hence rods alone are involved in the analysis of this paper.

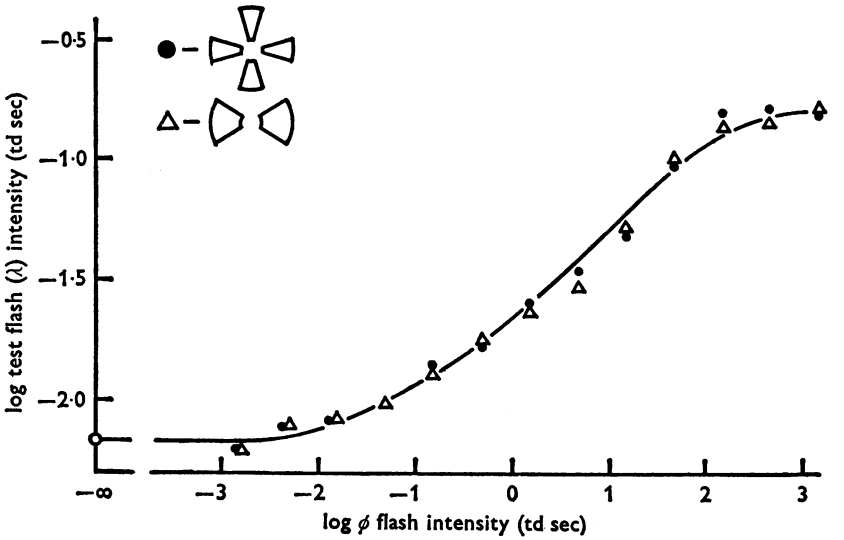

Fig. 7. Effect of varying the position of the windmill vanes on the threshold for seeing λ at different ϕ flash intensities. The circles show measurements made in the usual way, triangles when the vertical vanes were rotated so as to touch the horizontal vanes (see inset).

(*b*) Often at the beginning of a series of experiments the centre (and the surround) were bleached with a strong white light of say 7·3 log td sec which bleaches 90 % of rhodopsin if delivered within 45 sec. After 7 min when the cones had fully recovered and the rod threshold still lay far above them, the cone threshold could be measured in the conditions of the experiments to be performed, so that cone levels were known in advance. In the subsequent experiment the λ threshold always lay below this cone level and hence only rods were involved.

The windmill background

A cardinal feature of the present analysis, in the transformation from the non-uniform staircase of Fig. 4*a* to the uniform one of Fig. 4*b*, is that when the inhibitory surround has only four sectors instead of thirty-two (Fig. 2*b*) the signal N will be reduced by 8, the area factor. It is unlikely that this can be exactly true. If a sector can inhibit the centre, it can probably inhibit its neighbour, so the tightly packed thirty-two sectors which constitute the whole surround are probably each a little weaker in their effect upon the centre than one of the four sectors of the windmill (equally illuminated) due to the closeness of their mutual inhibition. However the mutual and the central inhibition are very unlike since ϕ flashes are bright and λ flashes are dim.

To test whether mutual inhibition had any detectable effect on the λ threshold we performed the experiment of Fig. 7. The horizontal sails of the windmill were kept fixed and the vertical pair could be set either vertical (as usual) or rotated so as to lie horizontal, contiguous with the other pair. The mutual inhibition would be minimal in the first and maximal in the second position. The black circles and white triangles of Fig. 7 show that log λ is not much influenced by the difference in position. Since there is no appreciable difference at any ϕ intensity between the inhibition produced when the vanes are as close as possible or as distant as possible, we are probably not far out in assuming that the inhibitory nerve signal N is always proportional to sector area. We have not investigated the relation of N to the fraction of surround area illuminated by ϕ extensively enough to define where (if anywhere) the rule of proportionality breaks down. Our aim has been to analyse the N signal, and for that purpose to use the 'windmill stop' to cause a large, but reliable reduction in N, a well measured reduction in λ threshold clear of experimental fluctuations. The distinct separation between the white and black circles of Fig. 4*a* shows that we have done this.

However, to satisfy ourselves that our analysis does not in the least rest upon the particular '$\frac{1}{8}$ windmill stop' chosen, we have sometimes used windmills with wider sails (e.g. $\frac{1}{2}$ or $\frac{1}{4}$ instead of $\frac{1}{8}$). It was always found when the surround area was reduced to a fraction $1/n$ that the flash ϕ had to be increased n times for λ to be maintained at threshold. Thus the conclusion of this paper can be derived from experiments with any size of windmill, but large sails will result in less separation of the Fig. 4*a* curves and so the 'staircase' will be less reliable. Very narrow windmill sails, on the other hand, raise questions as to optical precision of their retinal image which we believe are not serious with our 11° sails.

CONCLUSIONS

We have one conclusion, and found it very unexpected. It is that quanta caught by rods from a 100 msec flash are linearly encoded into an inhibitory signal N over a 10^4 range viz. from 1 quantum caught per 100 rods to about 300 per rod. Above this level saturation sets in. The relation is seen in Fig. 4*b* which plots log N against log ϕ and is replotted in Fig. 4*c* to display N against log ϕ.

In this form the curve resembles the cone potentials or S-potentials (in cases where only one pigment is involved) displayed as usual, with mV vertically against log light.

The resemblance is rather exact and hardly fortuitous. Naka & Rushton (1966) showed that S-potentials followed closely the relation.

$$V/V_\infty = I/(I+\sigma), \quad (2)$$

where V is the potential, V_∞ its maximum value, I the light energy and σ the value of I when $V = \frac{1}{2}V_\infty$, the semi-saturation light level. Naka (1969) in a computer-processed study of great exactness has shown eqn. (2) to be exceedingly closely followed. Tomita (1968) has shown the same relation for cone potentials in the gold fish, M. G. F. Fuortes (private communication) has found it for cones in the turtle, and Werblin & Dowling (1969) record the same relation from bipolar cells in the mudpuppy.

The curve of Fig. 4*c* is exactly the plot against log I of eqn. (2). The logarithm of the ordinates is exactly the curve of Fig. 4*b* which in turn is the transform of the curves of Fig. 4*a*. If it is considered that those 4*a* curves adequately fit the points, then those points lead to a signal generated by light according to eqn. (2).

We began to take our extraordinary signals more seriously when we found that the curve of signal against log light was precisely of the form found by micro-electrodes in several of the early stages in the long nerve path from receptor to brain.

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APPENDIX

Note on labelling of curves

Equation (2) is found so frequently in records from cells in the outer layers of the retina describing the response to light at various intensities, that it is worth having a label for the three curves that are useful in displaying the results. When the results are plotted simply as V against I (as in the analysis of Naka & Rushton (1967),

Fig. 4), we may call that particular hyperbola an 'H_0 curve'. When V is plotted against log I as in Fig. 4*c* of this paper we may call that $\tan h$ curve an 'H_1 curve'. When log V is plotted against log I as in Fig. 4*b* we may call the double log plot an 'H_2 curve'. H_0, H_1 and H_2 all plot the same relation (eqn. 2) but display it differently by using logarithmic rather than linear scales on neither, one or two axes respectively.

The familiar increment threshold curve which plots Fechner's formula

$$\Delta I = K(I + I_D)$$

against log I is our curve H_2 turned upside down as log ΔI. It may therefore be called an 'H_{-2} curve', since it is H_2 with both axes negative.

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