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EXCITATION IN THE GOLDFISH RETINA: EVIDENCE FOR A NON-LINEAR INTENSITY CODE

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SUMMARY

1. Experiments were done on isolated photopic goldfish retinas. They were stimulated by brief flashes of red light, and the spike activity of single ganglion cells was monitored by micro-electrodes. Red-ON-units were used exclusively.

2. The spatial integration of intensity was investigated using concentric disks of various diameters. Under these conditions, Ricco's relation (1877) was obtained.

3. Two small spots of light were positioned on two equisensitive sites in the receptive field; the (equal) intensities of both were varied in unison, and the responses recorded. An identical response was evoked by simultaneous illumination of both sites with an intensity, I, or by illumination of a single one of the sites with an intensity, KI. K always exceeded 2 (it averaged about 4) and it was constant in any one experiment.

4. The analysis of these results employed the assumption that an hypothetical quantity, the excitation, intervenes between the stimulus (light intensity) and the response (spike train). The excitation is a function of intensity, and it determines the response. The excitation from two spots is assumed to be twice that from one.

5. It was inferred that the excitation (E) was a power function of the intensity (I): $E = CI^n$, in which C and n are constants. The exponent, n, was always less than unity.

6. Two other experiments tested the predictive value of this inference. It accurately predicted the responses to a single spot anywhere in the field, and to two unequal intensities simultaneously illuminating two equisensitive sites.

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INTRODUCTION

Early in the history of recording from the optic nerve of vertebrates, Adrian & Matthews (1928) found that in general each nerve fibre was connected to a large number of photoreceptors. When Hartline (1938) succeeded in isolating single fibres in the frog's retina, he was able to map the actual receptive field, and he found that it included hundreds, perhaps thousands, of receptors. Kuffler (1952) in the cat and Barlow (1953) in the frog showed independently that the receptive field was organized on the basis of a central area surrounded by an antagonistic region. Wagner, MacNichol & Wolbarsht (1960) showed that in the goldfish, these opposing areas overlapped and were often colour-coded.

The question taken up in this paper relates to the fairly uniform centre of a red-sensitive field in the goldfish. It is certain that the receptors in this region add in some way their excitatory contributions to the ganglion cell, for if the area illuminated is reduced, the nerve discharge is diminished, and the intensity of light must be increased to restore it. Indeed, there is good evidence of a reciprocal relation between the threshold intensity of the light and the area upon which it falls—Ricco's law (1877). Consequently, many have concluded that when light falls upon Ricco's area, only the total quantum catch is significant for excitation, the spatial distribution of the light being irrelevant. This is certainly the simplest interpretation of Ricco's relation, but not the only one, and the object of this paper is to test its validity.

There are two parts. The first sets out the basic results, analysis, and conclusions. The second tests their predictive value.

PART I: A COMPARISON OF ONE- AND TWO-SPOT STIMULI

This part describes an examination of the importance of the stimulus light's spatial distribution. It was varied either by changing the diameter of a single stimulus disk or by changing the number of spatially separate spots which fell on equally sensitive regions of the receptive field.

METHODS

The experiments were carried out on goldfish retinal ganglion cells which were stimulated by red light and monitored by a micro-electrode. The preparation, the stimulator, and the recording system are very similar to those used by Wagner *et al.* (1960), and only a brief outline will be given here.

The retinas were isolated from the pigmented epithelium in room light and placed, receptor-side up, in a moist chamber mounted on a microscope stage. The chamber itself had a glass

bottom, and the light from the dual-beam stimulator entered through it. The retinal stimulus was directly observable through the microscope, and its sharpness of focus on the receptors was controlled by adjusting the position of a lens. The micro-electrode entered the retina through the receptor layer to come into electrical contact with a single ganglion cell. The spikes were amplified conventionally and recorded on magnetic tape for later analysis.

Only those units which were excited by the onset of red light were used (red-ON-units). They responded in this same way to red light everywhere in the receptive field (Wagner *et al.* 1960). They usually had little (less than 2 spikes/sec) or no maintained activity in the dark. In general, no background lights were used; the stimuli fell on dark retinas.

In the two-spot experiments, the paired spots came from the same beam, passing through a metal slide with two holes drilled in it. When only one spot was employed, the other was closed off with black electrical tape. With this method, the slide's position was always fixed, so there was no danger of the stimuli shifting positions, and the intensities were necessarily the same.

Red stimuli were used exclusively, the light passing through either a gelatin filter (Wratten 29, which transmits wave-lengths longer than 620 nm) or an interference filter (Optics Technology Monopass with a maximum transmittance at 647 nm). The maximum intensity available through the latter filter was approximately 10^{13} quanta cm^{-2} sec^{-1}, while the transmission through the gelatin filter was 4 times more energetic in its effect on the red-sensitive mechanism. All intensities were attenuated by neutral-density wedges (Eastman, Type M carbon) and neutral-density filters (Optics Technology, deposited metal film). A precise knowledge of their optical densities in the red was essential to the analysis of the data, so they were calibrated on the stimulator by thermopile and photomultiplier at the plane of the retina.

Red stimuli were used because they could best drive the red-sensitive cones to the exclusion of others (Marks, 1965). The exposures were brief (0·05, 0·08 or 0·10 sec) because prolonged stimuli bring out lateral antagonistic influences (Barlow, Fitzhugh & Kuffler, 1957), and these were to be avoided for simplicity.

RESULTS

Concentric stimuli of different areas. After a unit's isolation and identification as a red-ON type, its receptive field was mapped by positioning a small spot at a number of sites and determining the threshold intensity at each. Figure 1*a* shows two profiles of the same unit's receptive field. The upright triangles give the thresholds along one line; the inverted triangles were obtained along a second, perpendicular to the first. The two traverses intersected at the field's centre (filled symbols). Evidently this field was approximately uniformly sensitive over a central region about 0·8 mm in diameter.

The spatial integration of light intensity was then investigated by using stimulus disks of various diameters, all centred at the field's centre. Each disk flashed several times at a given intensity, and the number of spikes in each response was recorded. The ordinate of Fig. 1*b* gives the mean values, the abscissa gives the log intensity of the stimuli, and the symbols denote the different diameters. Consider now the horizontal interrupted line. It cuts the continuous lines through circles, triangles, etc., at some specific value of log intensity. Clearly this intensity with the

diameter corresponding to that symbol resulted in the same response (five spikes). These values of log intensity are plotted against log diameter in Fig. 1*c* (circles). The continuous line is theoretical: the result expected if the input (E) to the ganglion cell from each incremental area (A) was given by

$$E = kIA, \tag{1}$$

where k is a position-dependent weighting constant. The value of k was obtained from the continuous line of Fig. 1*a*; it was constant over the

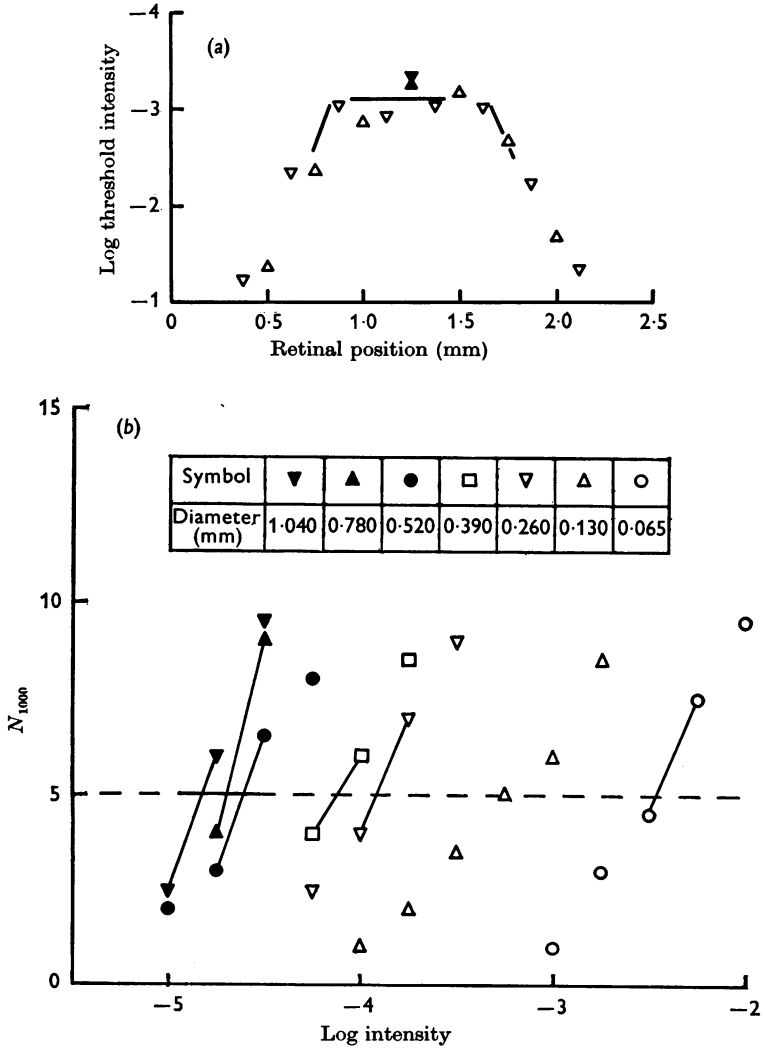

Fig. 1. For legend see opposite page.

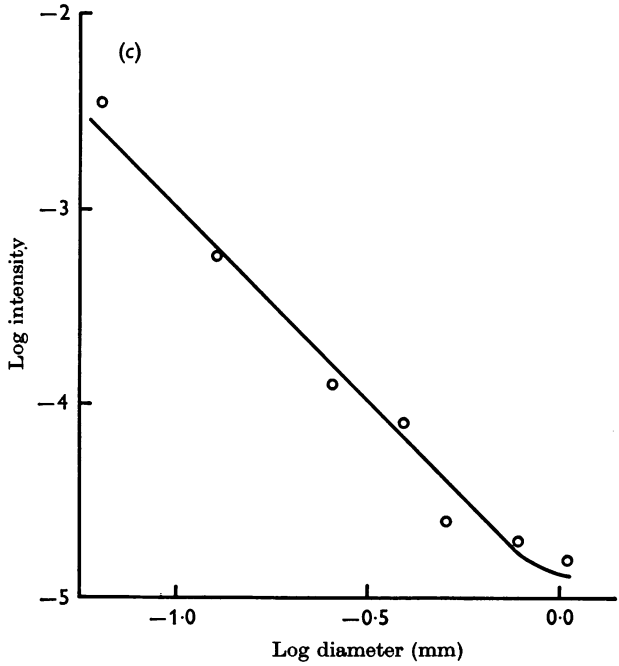

Fig. 1. Unit 26*N*. The stimulus in *a*, *b* and *c* was Wratten 29, 50 msec duration, at 10 sec intervals. (*a*) A single spot (0·065 mm diameter) was positioned at various sites along two lines perpendicular to one another, intersecting at the receptive field's centre (filled symbols). The upright triangles represent the log threshold along one of the lines, the inverted triangles apply to the other. (*b*) The stimulus disk was centred at the receptive field's centre. Its diameter and intensity were varied, and several responses to each stimulus were recorded. The mean values of the responses, measured by the number of spikes in the first second following onset of the stimulus, are plotted against the log intensity. The various diameters are symbolized as indicated in the inset. (*c*) This shows the log intensity which evoked five spikes as a function of the diameter of the disk it illuminated. The line has a slope of −2 over the central 0·800 mm.

central region 0·8 mm in diameter; hence over this region Ricco's law is predicted to hold. Figure 1*c* shows that it did, as Barlow (1953) and Wagner & Wolbarsht (1958) found in their studies of the frog's retinal ganglion cells.

Such a result leads to the hypothesis that a unit's response is determined by the product of the intensity and area of the stimulus, suitably weighted according to the sensitivity of the regions illuminated. If this were valid, then the geometry of the stimulus should be unimportant. The next section describes experiments which test this prediction.

Paired stimuli of equal area. The two-spot summation experiment was done as follows: After a unit was isolated, its receptive field was mapped

with small spots, and two equisensitive loci were chosen as test points. They lay on either side of the centre of the field, their centres separated from one another by some tenths of millimetres, e.g. 0·520 mm in the example of Fig. 2. Three sets of responses were obtained, one for each locus illuminated alone (Fig. 2*a*, upright and inverted triangles) and one for simultaneous illumination by identical intensities of both (Fig. 2*a*, circles). The responses to single stimuli were averaged and their mean values at each intensity are connected by the continuous straight lines in Fig. 2*a*.

Sites with similar thresholds also responded similarly to intensities above threshold, but it was never possible, in the limited time available, to find two sites which responded absolutely identically to all intensities. Generally, one was systematically more sensitive than the other, but never by more than about 0·1 log-unit. The stimuli were usually given in three ascending intensity series (e.g. left spot, right spot, both spots). The 10 sec interval between stimuli proved to be sufficiently long to prevent one response influencing the succeeding one. Long-term drifts in responsiveness were checked by giving standard stimuli at several times during the experiment. If the responses to these standards varied appreciably, the experiment was begun anew. If they continued to change, the unit was abandoned

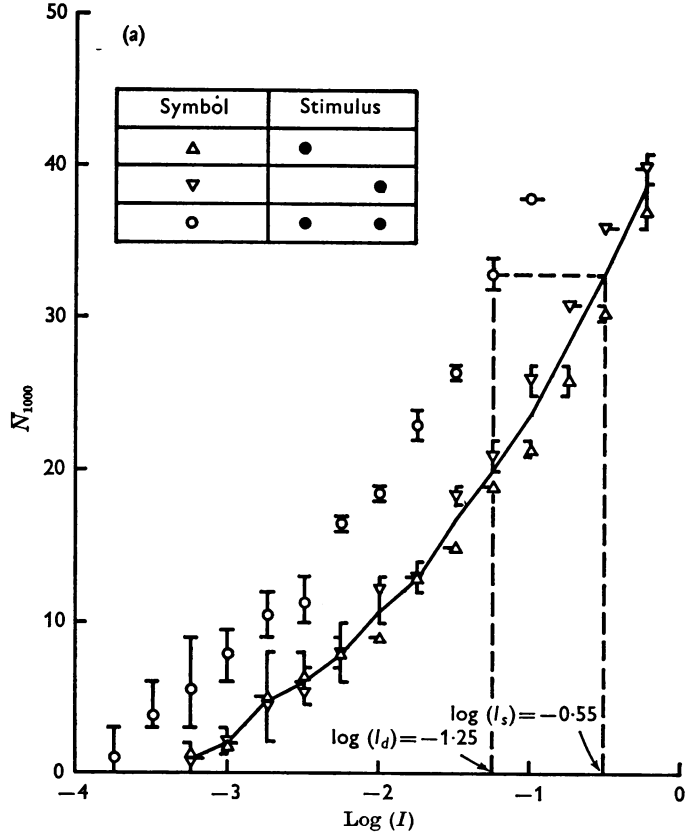

Fig. 2. For legend see opposite page.

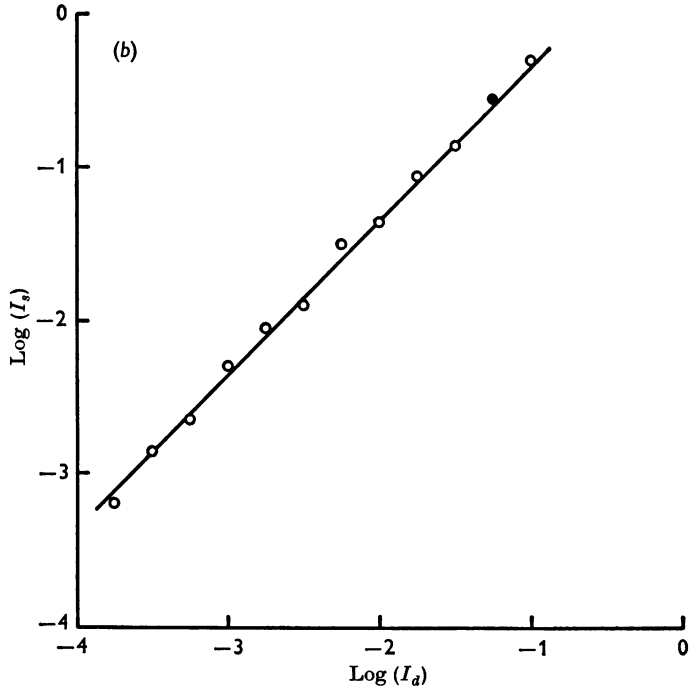

Fig. 2. Unit 28*N*. Two loci separated by 0·520 mm across the receptive field centre were illuminated either singly or simultaneously by spots (0·130 mm diameter, 80 msec duration, 10 sec intervals, 647 nm). (*a*) The responses to single stimuli: either the right or the left locus (upright or inverted triangles, respectively) was illuminated by an intensity, I_s, while the other was dark. Each point is the mean of 2–4 responses whose extreme values are given by the horizontal bars. The responses to double stimuli: both loci were illuminated simultaneously by an intensity I_d. Each circle is the mean of 2–4 responses. The continuous lines connect the means of the responses to single stimuli. In order to find what value of log (I_s) evoked the same response as some value of log (I_d), horizontal lines were drawn. For example, thirty-three spikes were evoked by: log (I_s) = −1·25, log (I_s) = −0·55. (*b*) The response–equalization plot: these points are the values of log (I_s) and log (I_d) which evoked the same response. The sample point (−1·25, −0·55) is filled.

The next step was a comparison of the responses evoked by single and double stimulation. Specifically, this question was asked: If intensity I_d (*d* for double) evoked a response of N spikes when it illuminated both sites, what intensity I_s (*s* for single) was required to evoke the same response when only one of the sites was illuminated? The set of intensity pairs (I_d, I_s) which evoked equal responses were then plotted on another graph, the response–equalization plot (Fig. 2*b*).

The 45° continuous line in this figure satisfies:

$$\log(I_s) = \log(I_d) + 0{\cdot}66, \qquad (2)$$

and the points fit it quite well (S.D. = 0·06). In other words, the response plots for stimulation by single and double spots had the same shape, since they were superimposable by a horizontal shift of 0·66 log-units. Identical experiments were done on a total of fifteen units, and Table 1 summarizes these data. Three additional points are relevant.

TABLE 1. Each column summarizes the results of one of the fifteen two-spot summation experiments. In row 4 the symbol > 620 indicates that the Wratten 29 gelatin filter was used. Rows 5–8 give the results obtained when all the intensity pairs in a given experiment were pooled. Rows 9–12 give similar measures obtained from a more restricted sample, which excluded the lowest value of $\log(I_d)$ and any others less than 0·5 log-units larger than it. $\bar{B}$ (rows 6 and 10) is the mean value of $\log(I_s)-\log(I_d)$ (equation 10); the standard deviation of the data from this mean appears in rows 7 and 11. Rows 8 and 12 give n, the exponent of the power function (equation 11)

1. Unit designation...	7*N*	8*N*	9*N*	10*N*	11*N*	12*N*	15*N*
2. Distance between the two spots' centres (mm)	0·80	0·80	0·80	0·80	0·57	0·38	0·25
3. Stimulus duration (sec)	0·10	0·10	0·10	0·10	0·10	0·10	0·10
4. Stimulus wave-length (nm)	> 620	> 620	> 620	> 620	> 620	> 620	> 620
Data from all intensities							
5. No. of intensity pairs	5	5	7	5	6	5	9
6. $\bar{B} = \overline{\Delta\log(I)}$	0·51	0·58	0·47	0·41	0·56	0·56	0·56
7. S.D.	0·10	0·15	0·08	0·11	0·18	0·08	0·20
8. $n = 0{\cdot}3/\bar{B}$	0·59	0·52	0·64	0·73	0·54	0·54	0·54
Data from high intensities							
9. No. of intensity pairs	4	4	5	4	5	4	7
10. $\bar{B} = \overline{\Delta\log(I)}$	0·46	0·65	0·46	0·46	0·60	0·59	0·59
11. S.D.	0·08	0·06	0·09	0·02	0·17	0·08	0·20
12. $n = 0{\cdot}3/\bar{B}$	0·65	0·46	0·65	0·65	0·50	0·51	0·51

1. Unit designation...	26*N*	27*N*	28*N*	31*N*	35*N*	38*N*	39*N*	40*N*
2. Distance between the two spots' centres (mm)	0·57	0·28	0·52	0·52	0·39	0·26	0·26	0·26
3. Stimulus duration (sec)	0·10	0·05	0·08	0·08	0·05	0·05	0·05	0·05
4. Stimulus wave-length (nm)	> 620	647	647	647	> 620	647	647	647
Data from all intensities								
5. No. of intensity pairs	7	6	12	10	12	12	11	9
6. $\bar{B} = \overline{\Delta\log(I)}$	0·58	0·66	0·66	0·67	0·44	0·51	0·61	0·53
7. S.D.	0·10	0·13	0·06	0·18	0·10	0·16	0·19	0·11
8. $n = 0{\cdot}3/\bar{B}$	0·52	0·45	0·45	0·45	0·68	0·59	0·49	0·57
Data from high intensities								
9. No. of intensity pairs	5	4	10	8	10	10	8	7
10. $\bar{B} = \overline{\Delta\log(I)}$	0·64	0·74	0·68	0·75	0·42	0·57	0·71	0·57
11. S.D.	0·04	0·05	0·05	0·10	0·08	0·10	0·14	0·09
12. $n = 0{\cdot}3/\bar{B}$	0·47	0·40	0·44	0·40	0·71	0·53	0·42	0·53

First, of the 130 intensity pairs recorded, 124 differed by more than 0·3 log-units, the amount predicted from Ricco's relation. The mean value for the unit of Fig. 1 was 0·58; the mean value for all units was 0·55, with extreme values of 0·10 and 0·95. These data were *t*-tested against the null hypothesis that 0·3 was the true mean, and this was rejected with a risk of error less than 0·0005. Any response which was evoked by a particular intensity of light on one spot could also be evoked by simultaneously illuminating both spots with light less than half as intense.

Secondly, most of the points did not conform to the best-fitting 45° line over so large a range as shown in Fig. 2*b*. Although the points at moderate-to-high intensities paralleled it from above, there was a systematic tendency of the points at lower intensities to lie below it, the ones at lowest intensity lying farthest below. Of the six values of $\Delta \log(I)$ which were 0·30 or less, five were from the low-intensity region of the response–equalization plot.

Rows 6 and 10 in Table 1 also illustrate this deviation. The former row includes information drawn from all the points in a given experiment, while the latter is from a more restricted sample which included only those points for which log (I_d) was 0·5 log-units or more greater than the minimum value of log (I_d). The mean values of $\Delta \log(I)$ in twelve of the fifteen cases were higher for the smaller samples. The standard deviation from the mean of the restricted sample was less than or equal to that of the larger sample in fourteen of the fifteen experiments (Rows 7 and 11). This indicates that the upper points fit a 45° line better than the sample as a whole.

Thirdly, the very simple relationship of equation (2) was also valid for other measures of the response. This is illustrated by Fig. 3, which was obtained as follows. All the individual responses from a particular unit were quantified by four numbers, N_{150}, N_{200}, N_{300}, and N_{1000}—the numbers of spikes fired by 150, 200, 300 and 1000 msec after onset of the stimulus. The fourth number always represents the total number of spikes in the response, and it appears on the abscissa; the first three are indicators of the time course, and they appear on the ordinate. The upper two sets have been displaced upwards for clarity. It will be noted that, in these graphs, intensity has disappeared, and only the characteristics of a response are plotted. The three kinds of symbols (upright and inverted triangles, circles) refer to the three kinds of stimuli, i.e. left spot alone, right spot alone, or both spots together. All the symbols in any one of the three categories clustered together, which implies that any two responses of equal N_{1000} were equal by these other criteria as well.

It should be noted, however, that this conclusion is valid only for the rather restricted set of conditions of the two-spot summation experiment. Other experiments showed that lengthening the duration of the stimulus profoundly affected the response's time course. For example, a discharge of twenty spikes which was caused by a 200 msec flash lasted much longer than one resulting from 80 msec of illumination. Its peak frequency was lower and its latency was longer. Increases in the area of a single spot also affected the time course, often resulting in bursts of activity separated by silent periods. And, as expected, a change in wave-length had an effect, particularly in colour-coded cells.

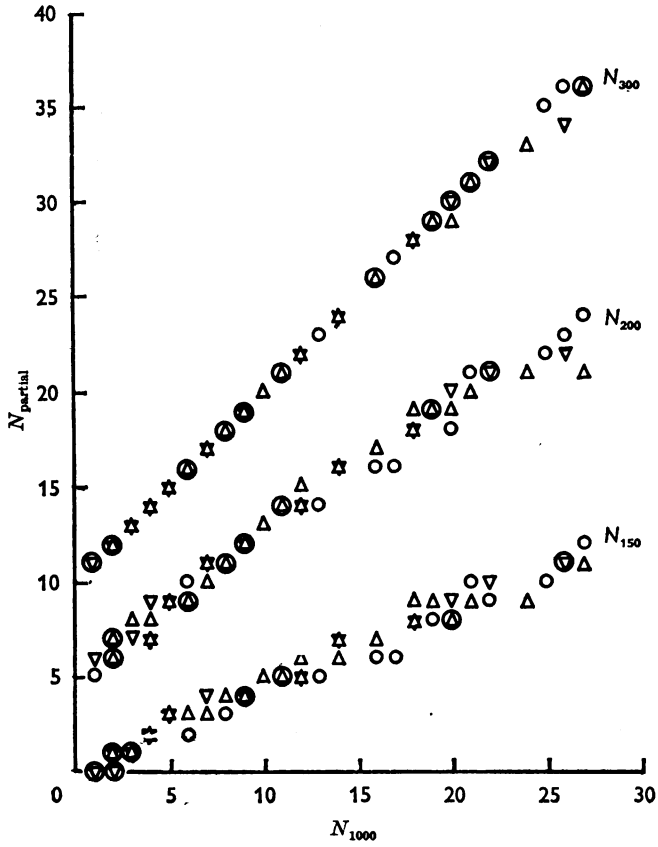

Fig. 3. Unit 31*N*. The stimulus conditions were identical to those in Fig. 2. Two spots flashed either alone (upright and inverted triangles) or together (circles). The three groups of symbols show (ordinates) the number of spikes fired by 150, 200 and 300 msec after stimulus onset. They are plotted against the total number of spikes in the response. Values of N_{200} and N_{300} have been displaced upward by five and ten spikes, respectively. Each point refers to a single response.

DISCUSSION

Ricco's relation and two spots. The results in the first two figures can be summarized by stating that less light was required for the same response when the light was distributed over disconnected areas. Doubling the area of a small stimulus disk is geometrically equivalent to adding a contiguous annulus to it, and Fig. 1 showed that the addition of an annulus was a less efficient method of increasing the response than was the addition of a separate spot (Fig. 2). It is of more than semantic interest to note that Ricco's relation is often called 'complete spatial summation' of

quanta, yet the two-spot stimulus resulted in summation still more efficient!

The neural mechanism underlying this increase in efficiency is unclear, but it must involve either the introduction of facilitatory influences or the removal of inhibitory ones. Lateral facilitation is unlikely, since the results require that it be less effective across small distances (Fig. 1) than longer ones (Fig. 2). A likelier guess is that inhibitory or occlusive interactions are involved, and that they are strongest over short distances, and therefore relatively absent when the two spots are spatially separate. If this interpretation is accepted, then the two-spot summation experiment becomes amenable to rather straightforward analysis.

The Analysis. Two assumptions are made.

First, it is assumed that the physical stimulus is translated neurally into an intermediate quantity, E, the excitation, which directly determines the ganglion cell's response. The physical nature of the excitation is unknown, but whenever two different physical stimuli evoke identical responses, they are said to generate equal amounts of excitation. This operationally defined quantity thus assumes the role of the intervening variable of physiological significance; it is the neural correlate of the physical stimulus. As such, it depends on all the variables which specify the stimulus, and on the state of the retina as well. But for the case in which only the intensity varies, one is justified in concentrating on this variable alone. Thus, an intensity at one locus (call it j) is coded into excitation

$$E_j = e(I_j). \tag{3}$$

This excitation function, e, is unknown. It includes all terms of lateral interaction within the stimulus disk itself.

Secondly, it is assumed that the excitation generated by simultaneous illumination of two spots is the sum of the excitations generated by either alone. Call the second locus k. Then

$$E_{j+k} = e(I_j) + e(I_k). \tag{4}$$

In other words, the two spots are assumed not to interact, for, if they did, a third term would be required on the right side of equation (4). This assumption of independent inputs cannot be completely justified, but it will be recalled that the two-spot experiment was designed to minimize lateral interactions. Furthermore, the data of Figs. 1 and 2 suggested that such interactions were in fact diminished when two spatially separate spots were used rather than one big spot of equal area.

The two-spot summation experiment deals with the special case in which the response to a single spot (of intensity I_s) equals the response to a

pair of spots (both of intensity I_d). I_s at one locus is coded into excitation

$$E_s = e(I_s), \tag{5}$$

which evokes a response, N_s. When I_d illuminates both loci simultaneously, the resulting excitation is

$$E_d = 2e(I_d), \tag{6}$$

which causes a response, N_d. When

$$N_s = N_d, \tag{7}$$

it follows that

$$E_s = E_d, \tag{8}$$

and substitution of equations (5) and (6) into equation (8) yields

$$e(I_s) = 2e(I_d). \tag{9}$$

The response–equalization plot (Fig. 2*b*) shows that

$$\log(I_s) = \log(I_d) + B, \tag{10}$$

where B is a constant. The problem now is to find what function, e, satisfies equations (9) and (10).

The solution is a power function

$$e(I) = CI^{(0{\cdot}3/B)} = CI^n. \tag{11}$$

C is a scaling constant, equal for two loci of equal sensitivities. (The author is indebted to Professors W. A. H. Rushton and W. B. Marks (personal communications) for the solution.)

Note that nothing was assumed about how the ganglion cell's *output* coded the intensity. This was avoided because the analysis dealt with the conditions necessary for a constant response—it was a null experiment.

The value of n is obtained from the y-intercept, B, in the response equalization plot:

$$n = 0{\cdot}3/B. \tag{12}$$

For the unit of Fig. 2,

$$n = 0{\cdot}3/(0{\cdot}66 \pm 0{\cdot}06) = 0{\cdot}45 \pm 0{\cdot}04. \tag{13}$$

Rows 8 and 12 in Table 1 give the other exponents so calculated. They are all less than unity, which indicates that the excitation continuum was a 'compressed' version of its physical correlate. The mean value of $\Delta\log(I)$ from all 130 samples was 0·55 log-units, which implies:

$$n_{\text{mean}} = 0{\cdot}30/0{\cdot}55 = 0{\cdot}55. \tag{14}$$

Clearly, if the excitation were a linear function of intensity, B would have been 0·30. It was not; the retina approximately took the square root of the intensity.

It was mentioned earlier that the fit in Fig. 2*b* was unusually good; more generally the upper points lay on a 45° line while the lower ones tended to curve downwards away from it. It can be shown quite easily that this deviation could result from the excitation having the form suggested by Stevens (1957):

$$e(I) = C(I-I_0)^n, \tag{15}$$

where C, n and I_0 are constants. For values of I much greater than I_0, it is indistinguishable from the simpler form (equation (11)), but for intensities near I_0 the two are very different.

If the response–equalization plot is consistent with the hypothesis that the excitation is a power function of intensity, what of the logarithmic function favoured by Fechner (1860)? It has the form

$$e(I) = C\log(I+I_0)+B, \tag{16}$$

in which C, B and I_0 are constants. In order to see how it would affect the response–equalization plot, it is necessary to substitute this expression into equation (8), which yields:

$$C\log(I_s+I_0)+B = 2[C\log(I_d+I_0)+B]. \tag{17}$$

When I_s and I_d are much larger than I_0, the expression reduces to:

$$\log(I_s) = 2\log(I_d)+B/C. \tag{18}$$

This prediction that the response–equalization plots should have a slope of 2 was never upheld, so these data fail to support the logarithmic hypothesis.

PART II: PREDICTIONS

The predictive value of Part I is tested below in two new experiments.

In the first, a single spot illuminates, one at a time, a number of loci in the receptive field. By hypothesis, the excitation from any one of them, say the jth site, is:

$$E_j = C_j I_j^n, \tag{19}$$

where C_j is a position-dependent weighting constant. A response will be evoked by I_j at the jth site or by some generally different value, I_k, at the kth site. When the responses are the same, so are the excitations:

$$E_j = C_j I_j^{\,n} = C_k I_k^{\,n} = E_k. \tag{20}$$

It follows that

$$I_j^{\,n}/I_k^{\,n} = C_k/C_j \tag{21}$$

or

$$\log(I_j)-\log(I_k) = \text{constant}. \tag{22}$$

This relation should hold for all responses, and it is the first prediction; all the response plots should be superimposable on one another by a shift along the log intensity axis.

In the second experiment unequal intensities simultaneously illuminate two equisensitive sites (1 and 2). By hypothesis, the excitation from the pair is

$$E_d = CI_1^n + CI_2^n. \tag{23}$$

The two intensities always differed by a constant factor, M, hence

$$E_d = C(1 + M^{1/n})I_1^n. \tag{24}$$

By the same reasoning that was used in the preceding paragraph, the response plot for the pair, when plotted against (log I_1), should be horizontally superimposable upon all the other response plots, i.e. for any value of M. Furthermore, the exact position along the horizontal axis can be predicted, if n and M are known.

METHODS

The two-spot experiment employed both of the stimulator's beams, one spot coming from each. Both had the same dominant wave-length (647 nm), one set by the interference filter, the other by a grating monochromator. The luminous energies of the two spots were equated early in the experiment by alternately flashing them on the same site and adjusting the wedges to make the two evoke equal responses. This difference in wedge setting was taken into account in all the manipulations thereafter.

RESULTS

One spot. Figure 4 is a family of response plots with retinal position as parameter, and all other components of the stimulus fixed. The same empirical curve was fitted to each set of symbols, and in all cases the fit is quite good. Similar families were obtained from nine units in all, and in every case the points fit a common template about as well as the example shown. All the templates had the same general shape. The time courses of the responses were investigated as in Fig. 3, and they were found to be similar; that is, responses with similar N_{1000} had similar time courses.

To summarize, the response plots from all loci were superimposable on one another by a shift along the log intensity axis, as predicted.

Two spots. The next results were obtained after completion of a standard two-spot summation experiment, in which the value of n was found to be 0·57 (unit $40N$).

The responses shown in Fig. 5*a* were all evoked by double stimulation at two equisensitive sites (1 and 2). The abscissa gives the log intensity at 1, but the relative value at 2 differed for the various symbols. In the case of

the circles, the two intensities were equal, while the upright triangles, the inverted triangles, and the squares apply to stimuli in which the intensity at 2 was larger by 0·25, 0·50 and 0·75 log-units, respectively. As expected, the same response was evoked by a smaller intensity at 1 when it was accompanied by a larger intensity at 2. Or, to phrase it in graphic terms,

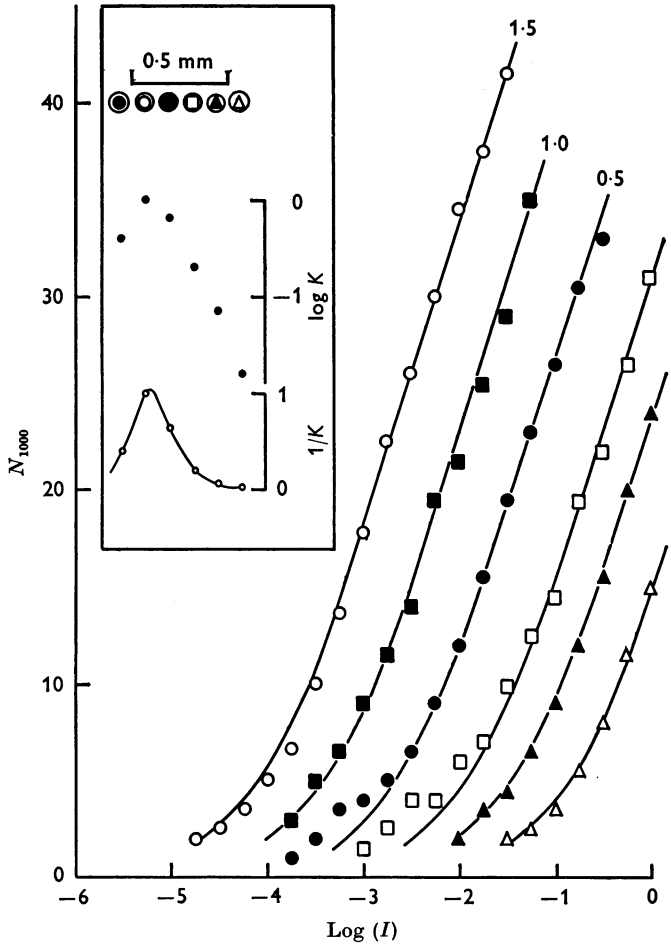

Fig. 4. Red-ON-unit: a family of response plots. The stimulus disk (0·130 mm diameter, 647 nm, 80 msec duration, beam 1) illuminated, one at a time, each of six positions schematized by the row of circles in the inset. The points for the three most sensitive loci have been shifted to the left, for clarity, by the amounts indicated at the top of each set of symbols. The same empirical template curve has been fitted by eye to all six sets of points. Inset: the horizontal separation between the response plot of the most sensitive position and the response plot for any other position is called log (K). The value of $-\log(K)$ and of $1/K$ are plotted as functions of position.

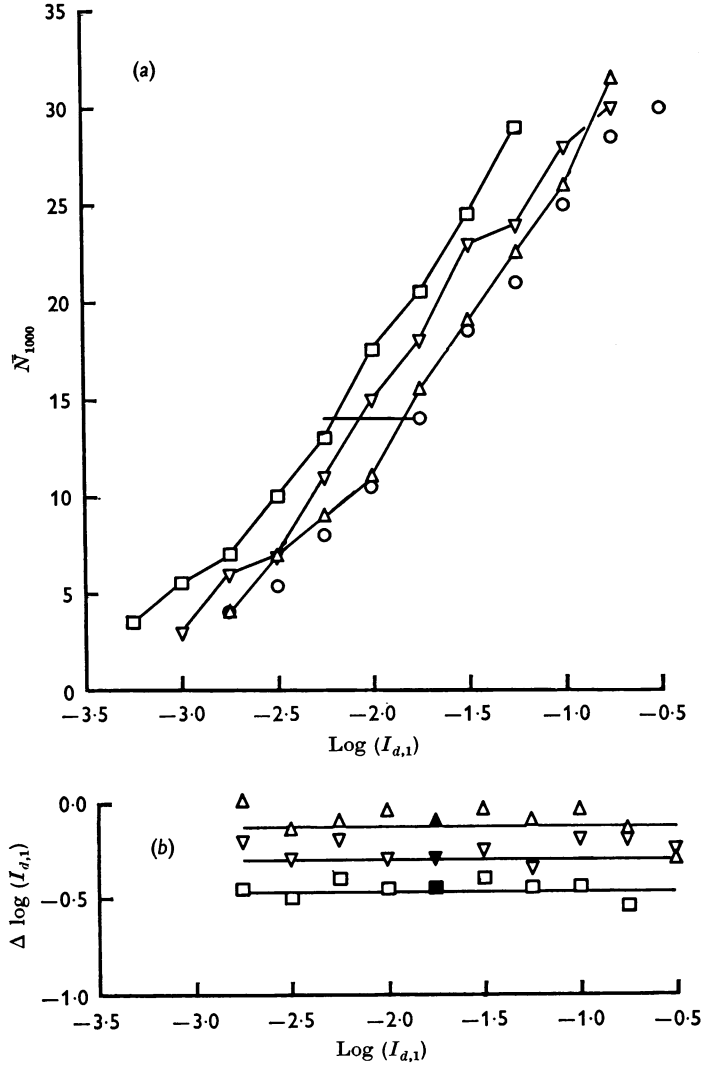

Fig. 5. Unit 40*N*. The two spots (0·130 mm diameter, 647 nm, 50 msec duration, 10 sec intervals) were separated across the receptive field's centre by 0·260 mm. They illuminated sites 1 and 2. (*a*) These responses apply to four arrangements of double stimulation; in all cases, the responses are plotted against the log intensity at site 1. The intensity at 2 flashed synchronously and was either equal to that at 1 (circles) or else exceeded it by 0·25, 0·50 or 0·75 log-units (upright triangles, inverted triangles, and squares, respectively). (*b*) The abscissa is the same as in *a*; the ordinate gives the amount of leftward shift in *a* as the intensity at site 2 increased parametrically. The three intersections of the sample horizontal line in *a* are plotted as filled symbols in *b*. The three horizontal lines give theoretical values.

the responses moved to the left on the graph as the intensity at 2 increased parametrically.

The amount of leftward shift of the responses was examined in the following way. Straight connecting lines were drawn between similar symbols, and then a horizontal line through each circle intersected the connecting lines, thus yielding a graphical answer to the question: What log intensity at 1 ($\log(I_{d,1})$) evoked the criterion response when accompanied by different values of $\log(I_{d,2})$? One horizontal has been drawn as an example and its three points of intersection (estimated to the nearest 0·05 log-unit) give the answers for a response of 14·0 spikes:

$\log(I_{d,1}) = -1{\cdot}75$, $\log(I_{d,2}) = -1{\cdot}75$, circles;
$\log(I_{d,1}) = -1{\cdot}85$, $\log(I_{d,2}) = -1{\cdot}60$, upright triangles;
$\log(I_{d,1}) = -2{\cdot}05$, $\log(I_{d,2}) = -1{\cdot}55$, inverted triangles;
$\log(I_{d,1}) = -2{\cdot}20$, $\log(I_{d,2}) = -1{\cdot}45$, squares.

The latter three of these sample values represent changes in $\log(I_{d,1})$ of $-0{\cdot}10$, $-0{\cdot}30$ and $-0{\cdot}45$ log-units. These differences are plotted as filled symbols in Fig. 5*b*, whose abscissa is the same as in *a*. Thus, a shift to the left in *a* appears as a downward shift in *b*. The symbols have the same meanings in both halves of the figure, but the circles have been omitted in the second, since they define the standard horizontal line at the ordinate's zero. The experimental points scatter, but they do not show any systematic tendency to slope up or down. This constancy is in accord with the prediction. When their values were averaged for each set of symbols, their means and standard deviations were $-0{\cdot}11 \pm 0{\cdot}08$, $-0{\cdot}26 \pm 0{\cdot}06$ and $-0{\cdot}46 \pm 0{\cdot}05$. The predicted values ($-0{\cdot}14$, $-0{\cdot}30$, $-0{\cdot}47$) are given by the continuous lines; they all lie well within the standard deviations, indicating that the results are consistent with prediction.

Similar experiments were done on three units, always with comparable results.

DISCUSSION

Figure 4 is in accord with the predictions, and a different result would have invalidated the model. But the results are also consistent with any model in which the (linear) intensity is weighted according to its position before being transformed by an excitation function. The data do not allow one to decide if (K), the empirical constants, are related to (C), the weighting constants of the theory.

On the other hand, Fig. 5 allows exclusion of other models which the earlier data did not. For instance, the results of the *standard* two-spot experiment could have been interpreted by assuming a particular excitation function and inferring the kind of non-linear summation which would

account for the experimental results. (It will be recalled that the opposite was done; linear summation was assumed, and the non-linear excitation was inferred.) For instance, the results of Fig. 2 would be explained equally well if it were assumed that

$$e(I) = \log(I) \tag{25}$$

and that the summation of E_1 and E_2 were done by the following rule:

$$E = \tfrac{1}{2}(E_1+E_2)\left[1+\frac{|E_1-E_2|}{E_1+E_2}\right]+B\left[1-\frac{|E_1-E_2|}{E_1+E_2}\right]. \tag{26}$$

But this alternate scheme will not predict the result of Fig. 5*b*. Instead, it predicts that $\Delta\log(I)$ changes from $-\log(M)$ at low intensities to $(-B-\log(M))$ as the intensity increases. It will be recalled that $\log(M)$ took the values 0·25, 0·50 and 0·75, but a glance at Fig. 5*b* shows that all the observed displacements were much smaller than these supposed minimum values.

It is probably possible to generate a still more complex form of non-linear summation which would reconcile this kind of two-spot summation experiment with a linear or a logarithmic transformation. But it seems justified to accept the simpler interpretation at this point, and to conclude that the intensity at each locus was transformed by a power function and that these two quantities summed linearly to drive the ganglion cell.

Anatomical correlates. The sites of the compression and summation are unknown. The ganglion cell's axon hillock seems a good candidate for the latter function, but the former could be almost anywhere. A hint was provided by Svaetichin, Krattenmacher & Laufer (1960), who worked on the fish's isolated retina. They reported that a pencil of rays sharply focused on to one cone evoked a much smaller L-response than it did when defocused to illuminate ten cones. Since the L-responses are known to come from structures distal to the ganglion cells (MacNichol & Svaetichin, 1958), this finding implies that the compression is done there too.

A number of workers have suggested that the compression is a receptor phenomenon. The psychophysical results of Stevens, Carton & Schickman (1958) and the electrophysiological results of MacNichol (1956), Werner & Mountcastle (1965) and Tapper (1965) are particularly relevant. One is tempted to argue (by analogy with the sensory systems studied by these other authors) that the compression in the vertebrate visual system occurs in the rods and cones. This is probably unjustified, as Enroth-Cugell & Robson (1966) have demonstrated that in some ganglion cells of the cat, intensity was coded linearly. Since both linear and non-linear ganglion cells probably shared many of the same receptors, this finding suggests that the non-linearity, when present, lies central to the receptors.

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