

QUANTITATIVE ANALYSIS OF CAT RETINAL GANGLION CELL RESPONSE TO VISUAL STIMULI

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IN A RECENT paper, RODIECK and STONE (1965a) investigated the response of cat retinal ganglion cells to moving visual stimuli. Averaging techniques enabled the responses to be studied quantitatively. These observers were interested in discovering whether the results they obtained could be interpreted quantitatively in terms of the known properties of the receptive fields of retinal ganglion cells. To do this, however, it was necessary to know quantitatively the relevant receptive field parameters. A study aimed at quantifying certain parameters of a ganglion cell's response to small flashing spots of light was undertaken and the findings presented (RODIECK and STONE, 1965b).

The present paper is based on the experimental findings in the above two papers. The general aim of the present work was to test the consistency of the experimental data. In so doing it has been found possible to demonstrate a close and quantitative relationship between the response of a retinal ganglion cell to small flashing spots of light and its response to moving visual stimuli.

I. EXPERIMENTAL FINDINGS

Moving figures

Either a white figure moved across the receptive field of an ON-centre unit, or a black figure moved across the receptive field of an OFF-centre unit, produced the same type of averaged response pattern which we refer to as the "centre activated" (CA) type (RODIECK and STONE, 1965a). For thin rectangular bars the activation of the unit was unimodal as the bar passed over the receptive field. For wide bars the activation was bimodal, the first peak being larger than the second. An initial suppression was usually seen as a figure moved into a receptive field. A larger suppression was invariably present as the figure left the receptive field. This suppression was often followed by a small activation before the unit returned to its maintained firing rate.

Either a white figure moved across the receptive field of an OFF-centre unit, or a black figure moved across the receptive field of an ON-centre unit, produced the same type of averaged response pattern which we refer to as the "centre suppressed" (CS) type. The "CS" type of response pattern is the reverse of the "CA" type. For thin rectangular bars the suppression of the unit, as the bar passed over it, was unimodal, but was bimodal for large bars if the level of maintained activity was high enough. An initial activation was usually seen as a figure moved into a receptive field. A larger activation was invariably present as the figure left the receptive field. This activation was often followed by a small suppression before the unit returned to its maintained (unstimulated) firing rate.

These findings are illustrated schematically in Fig. 1 for the movement of a wide bar. The "CA" and "CS" response types appear to be derived from a continuous curve which we call the "response curve". As drawn, this curve must be inverted and pushed up by a maintained firing level to obtain the "CS" type response. The response curve thus reflects the change in the maintained firing rate of a unit to a visual stimulus.

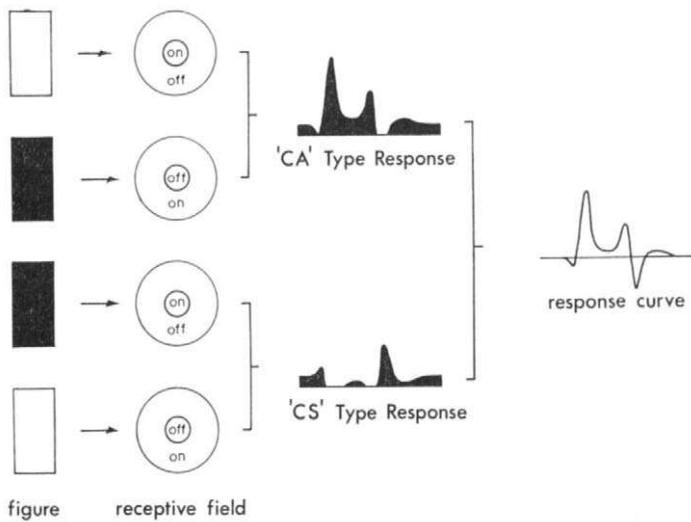


FIG. 1. Schematic illustration of the characteristic response of a retinal ganglion cell to a wide bar moved through its receptive field. This figure is based upon experimental findings presented elsewhere (RODIECK and STONE, 1965a).

Small flashing spots of light

RODIECK and STONE's findings using averaging techniques (1965b) are extensions of those originally described by KUFFLER (1953). Figure 2 illustrates schematically the response of an ON-type region to a small (2'-4') flashing spot of light. Some variability was seen in the many averaged response histograms compiled, and this diagram illustrates the typical properties of these responses. The stimulus is shown in the lower left as a light turned on and later off. The typical response of an ON-type region was a transient increase in the firing rate as the light turned on, decaying to a maintained rate higher than that before the light turned on. When the light turned off there was a transient suppression of firing, followed by a return to the original firing rate. The diagram shows schematically the firing pattern of a single response and, above it, an averaged response histogram compiled from the responses to many repetitions of this stimulus. OFF-type responses are similar except that the unit is suppressed when the light is flashed on and activated when it is flashed off. The top diagram illustrates the inferred response curve to this stimulus.

A flashing light may be viewed as two alternating stimuli. The first is a step increase in the illumination and the second a step decrease in the illumination. Thus, as shown schematically in the right of Fig. 2, a step change in illumination results in a step change in firing rate plus a transient change in firing rate.

The curve of amplitude of response to a step change in illumination, plotted as a function of position along a diameter of a receptive field, is triphasic. For an ON-centre unit and a positive step in illumination the middle of this triphasic curve is positive, and its ends,

corresponding to the surround, are negative. At the zero crossing of the triphasic curve either no response was obtained, or a weak "ON-OFF" response. As will be shown in the present paper, ON-OFF responses do not significantly contribute to the response of a unit to a moving figure. We call this triphasic curve the "shape" of the receptive field.

Small moving spots of light

Observations relating to small moving spots of light (RODIECK and STONE, 1965b) may be summarized by stating that small ($\leq \frac{1}{2}^{\circ}$) movement of a small spot of light proved to be a very effective stimulus, causing a change in the firing rate proportional to the gradient of the shape of the receptive field along the path of the spot.

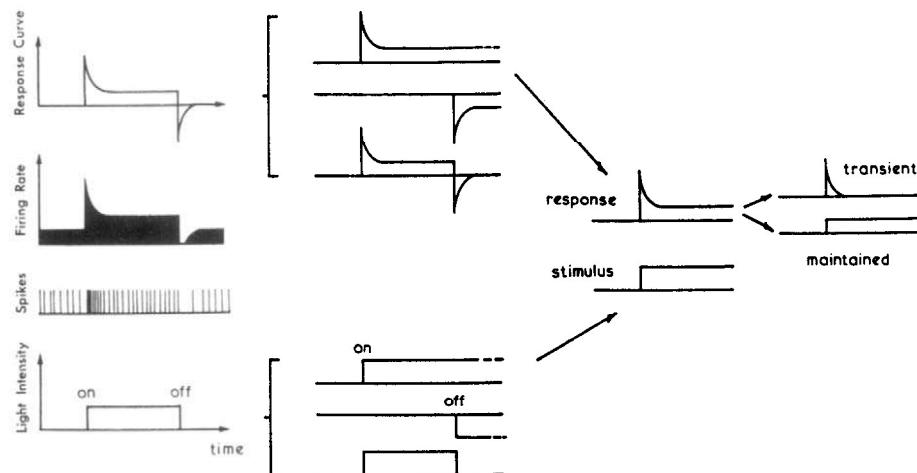


FIG. 2. Schematic illustration of the characteristic response of a retinal ganglion cell to a flashing light. This figure is based upon experimental findings presented elsewhere (RODIECK and STONE, 1965b).

Superposition

Under certain conditions, the response patterns of a retinal ganglion cell to two visual stimuli presented separately may be superimposed to give a good estimate of the response pattern of the cell to the two stimuli presented simultaneously (RODIECK and STONE, 1965b). The magnitude of the response is considered to be the difference between the firing rate during the presentation of a visual stimulus and the maintained firing rate.

II. QUANTITATIVE DESCRIPTION OF EXPERIMENTAL PARAMETERS

Implications of superposition

In this paper the assumption is made that superposition holds as the region of the receptive field over which each stimulus acts becomes small and the number of stimuli becomes large. This assumption is not in conflict with any of the results described previously. It is made because it allows certain mathematical simplifications of receptive field properties (BÉKÉSY, 1960). The actual justification for making the assumption, however, must come from the consistency of the results to which it leads. Its relevance to the experimental results reviewed above may be seen in the following example:

Consider the movement of an arbitrary figure through the receptive field of a retinal ganglion cell as shown in Fig. 3. It may be imagined that there is a fine meshed wire screen between the moving figure and the cat so that the cat sees the figure moving behind the screen. Light passing through a hole in the screen is considered to be an individual stimulus acting on a discrete region of the receptive field. As the leading edge of the black triangle passes under a certain hole in the screen the light passing through the hole is reduced and remains so until the trailing edge of the figure passes across the hole and the previous illumination is resumed. Each individual stimulus is thus equivalent to a small light turned off and on over

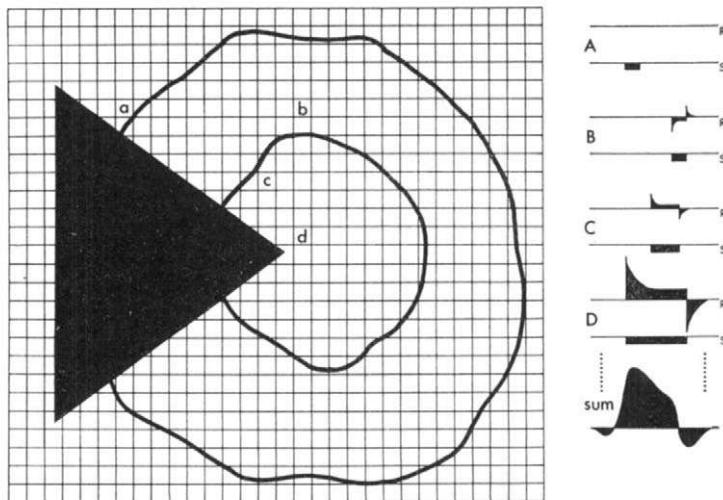


FIG. 3. Diagrammatic illustration of the proposed manner in which various parts of a retinal ganglion cell's receptive field contribute to its firing pattern (see text). The black triangular figure is moving to the right and, at different times, covers different parts of the receptive field shown. The contributions of four small regions in the visual field (the small squares labelled "a-d") are shown on the right. In each case the upper line (labelled "R") is the response component while the lower line (labelled "S") is the stimulus component. A: The tip of the triangle crossing square "a" causes a decrease in the luminance of this square as shown. No response component is produced, however, because square "a" lies outside the receptive field. B: At a later time the same part of the figure that covered square "a" now passes square "b" causing a similar decrease in the luminance of this square. Because square "b" is in the surround of the receptive field a response component characteristic of the surround is produced during this period. C: Square "c" is in the centre region but near the centre-surround border so that a weak centre-type response component is generated by the movement of the figure over this point. Compare time differences with those shown in A, B and D. D: Square "d" is near the centre of the receptive field and the movement of the figure over this square thus produces a strong centre-type response.

a small region of the visual field. (This is strictly true only in the limit as the hole becomes infinitely small; however, good approximation is realized for holes subtending a visual angle significantly smaller than that of the receptive field or figure. Thus the leading or trailing edge of a figure, moved at $10^\circ/\text{sec}$ past a $3'$ hole, crosses it in 5 msec.) The combination of all such component stimuli is equivalent to the movement of the triangular figure through the receptive field. If superposition holds then the response of the cell to each of these component stimuli may be summed (as shown diagrammatically in the right half of Fig. 3), to provide the response pattern of the cell to the moving figure. If the velocity of the figure

increases, the time during which the figure remains beneath a given hole correspondingly decreases. Thus, in general, if superposition holds it is possible to obtain, from the response patterns to a small light spot flashed in various parts of a cell's receptive field, the response pattern of the cell to any shaped figure at any orientation moving at any velocity through any part of the receptive field.

Equation of superposition

In Fig. 4 an arbitrary figure is shown in its position at time $t=0$. It is assumed to be moving to the right with a velocity v . The response of the unit to the moving figure may be considered to be made up of two components. The first component is due to the leading

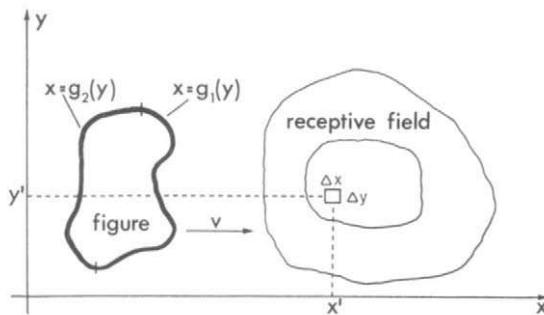


FIG. 4. Variables used in derivation of superposition integral for moving figures.

edge of the figure passing over the receptive field, and the second to the trailing edge passing over the receptive field. $g_1(y)$ and $g_2(y)$ describe respectively the leading and trailing edges of the figure. For simplicity it will be assumed that the figure is simple in the sense that $g_1(y)$ and $g_2(y)$ are single valued (i.e. there is only one leading and one trailing edge). In any small area of the receptive field ($\Delta x \Delta y$) the leading edge of the figure may be considered to be a positive step function of intensity in time, and the trailing edge a negative step function of the same magnitude which returns the illumination to the previous value.

Let the response component to a step change in illumination in the small area $\Delta x' \Delta y'$ at position (x', y') be represented by the function

$$f(x', y', t) \Delta x' \Delta y'$$

and the times at which the leading and trailing edges of the figure cross this point be t_1 and t_2 respectively. The response component to the positive step of the leading edge is therefore

$$f(x', y', t - t_1) \Delta x' \Delta y'$$

while the response component of the negative step of the trailing edge is

$$-f(x', y', t - t_2) \Delta x' \Delta y'$$

The total response component from this area is therefore:

$$[f(x', y', t - t_1) - f(x', y', t - t_2)] \Delta x' \Delta y'$$

and the sum of all such areas of the receptive field is:

$$R(t) = \sum_{-\infty}^{+\infty} \sum_{-\infty}^{+\infty} [f(x', y', t - (x' - g_1(y'))/v) - f(x', y', t - (x' - g_2(y'))/v)] \Delta x' \Delta y'$$

Where the edges of the figure are taken to be at $g_1(y')$ at $t=0$. In the limit as the area of each response component becomes diminishingly small the equation for the response becomes:

$$R(t) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} [f(x, y, t - (x - g_1(y))/v) - f(x, y, t - (x - g_2(y))/v)].dx dy$$

Analytical representation of the receptive field

a. *Separation of variables.* As a first step towards solving the response equation it is assumed that $f(x, y, t)$ can be expressed as the product of a spatial and a temporal term:

$$f(x, y, t) = f(x, y).h(t)$$

In other words it is assumed that the form of the temporal response is invariant over the receptive field. The magnitude of the temporal response at any point in the receptive field is given by $f(x, y)$ which is the "shape" of the receptive field. This assumption is a simplification of the experimental data (RODIECK and STONE, 1965b). To the extent that the shape of the transient term or the ratio of the transient to maintained terms vary over the receptive field (that is are functions of x and y) the product separation of $f(x, y, t)$ must serve only as an approximation to the actual situation. This will be discussed in greater detail later. The resulting expression for $R(t)$ is:

$$R(t) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} f(x, y)[h(t - x/v + g_1(y)/v) - h(t - x/v + g_2(y)/v)].dx dy$$

Note that the centre integral is in the form of a convolution of the shape of the receptive field, $f(x, y)$, with a term which, in turn, is the convolution of the first derivative of the shape of the figure with the temporal step response of the unit. This is in agreement with Békésy's comment (1960) that if the system is linear then what he calls the "sensation magnitude" (response curve), for any given stimulus distribution, can be calculated by the convolution integral if the "neural unit" (receptive field) is known. To solve this equation it is necessary to specify both $f(x, y)$ and $h(t)$. In choosing specific functions it is useful to select functions which represent the experimental findings fairly well and are simple to operate with mathematically.

b. *The temporal factor.* As noted earlier, although some variation was seen, the response of a unit to a step change in illumination could be characterized by two components, a maintained change in the firing rate and a transient component which typically had an exponential-like decay. A mathematical expression which describes this change is:

$$h(t) = [m + t \exp(-\alpha t)]\mu_{-1}(t)$$

where m and t are, respectively, the magnitude of the maintained and transient components, α is the reciprocal time constant of the transient decay, and $\mu_{-1}(t)$ is the step function previously discussed and defined by the relation:

$$\mu_{-1}(t) = \begin{cases} 0 & \text{for } t < 0 \\ 1 & \text{for } t \geq 0 \end{cases}$$

This function is the simplest consistent with the data and is plotted in the upper left of Fig. 5. Other functions, having approximately the same shape will serve equally well.

c. *The spatial factor.* A function chosen to represent $f(x, y)$ must have certain basic properties to enable it to characterize the shape of the receptive field. Considering symmetry first, the receptive fields described by KUFFLER (1953) and RODIECK and STONE (1965b)

were approximately radially symmetric. As there seemed to be no consistent asymmetry from field to field the assumption of perfect radial symmetry is the simplest one consistent with the data. This implies that the variables x and y in the expression for $f(x, y)$ must occur together in the form $x^2 + y^2$.

Analysis of the relation between the response of a unit to a small flashing and a small oscillating spot of light demonstrated that there is no functional discontinuity in passing from the centre region to the antagonistic surround. The amplitudes of the maintained and

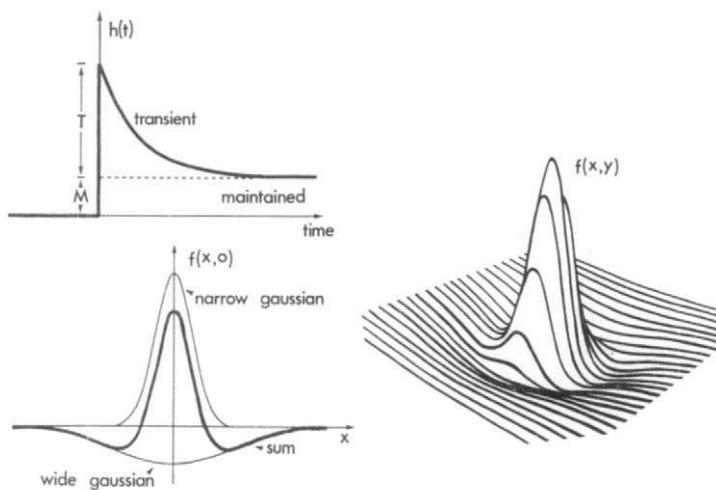


FIG. 5. Idealized receptive field properties (see text).

transient components of the response to a small flashing spot of light on a line through the centre of the receptive field are triphasic. Thus $f(x, 0)$ or $f(0, y)$ must also be triphasic. There are a number of functions which could be used to generate a triphasic curve. From the standpoint of adequately representing the data, most of these curves will serve. From the standpoint of mathematical simplicity, however, a convenient function to choose is the sum of two Gaussian functions, a positive one and a wider negative one as in Fig. 5.

The equation for $f(x, y)$ is then:

$$f(x, y) = g_1 \sigma_1^{-2} \pi^{-1} \exp(-(x^2 + y^2)/\sigma_1^{-2}) - g_2 \sigma_2^{-2} \pi^{-1} \exp(-(x^2 + y^2)/\sigma_2^{-2})$$

The factor $(1/\pi\sigma^2)$ is included in each term of the expression so that the integral of each term over all space is g . This function is plotted in perspective view in Fig. 5.

We shall adopt the convention that g_1 and g_2 are both positive. The first term of $f(x, y)$ is principally concerned with the central region of the receptive field, σ_1 being a measure of its width. Conversely the second term of $f(x, y)$ is principally concerned with the surround of the receptive field, and σ_2 is a measure of its width. Similarly the ratio of g_1 to g_2 is a measure of the ratio of the strength of the centre to the surround. The two terms of $f(x, y)$ need not, in themselves, have any physical significance, as it is only their difference that is presently considered. Evidence reviewed by Rodieck and Stone (1965b), however, suggests that the separation of the spatial factor into these two terms may reflect an underlying property of retinal organization. Either $f(x, y)$ or $h(t)$ may be normalized as it is their product alone which determines firing rate. Neither is normalized in the following

equations, however, so that the relationship between different factors may be more easily seen.

Substituting these values for $h(t)$ and $f(x, y)$ into the expression for $R(t)$ gives:

$$R(t) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} \{g_1\sigma_1^{-2}\pi^{-1}\exp(-(x^2 + y^2)/\sigma_1^{-2}) - g_2\sigma_2^{-2}\pi^{-1}\exp(-(x^2 + y^2)/\sigma_2^{-2})\} \\ \{m + t\exp[-\alpha(t - x/v + g_1(y)/v)]\mu_{-1}(t - x/v + g_1(y)/v) \\ - m + t\exp[-\alpha(t - x/v + g_2(y)/v)]\mu_{-1}(t - x/v + g_2(y)/v)\} dx dy$$

In this expression the response curve is a function of time. To express the response of a unit as a function of the position of the figure as it moves across the receptive field it is necessary to make the substitution $t=x/v$.

III. CALCULATED RESPONSE CURVES

Moving rectangular bars

a. *Equation.* Given the shape and velocity of a figure as well as its path across a receptive field, the above expression for $R(t)$ may be evaluated. For most figures an analytic solution is not possible and numerical methods must be employed. An analytic solution is possible, however, for the case of a "bar" of any width, moved across a receptive field in a direction perpendicular to the long axis of the bar as in Fig. 1. With the convention that at $x=0$ the centre of the bar coincides with the centre of the receptive field, and the assumption that the ends of the bar extend beyond the receptive field, the solution of the above equation as a function of the position of the bar is:

$$R(x) = \frac{1}{2}g_1m(\operatorname{erf}(x' + w') - \operatorname{erf}(x' - w') - \gamma\operatorname{erf}(\beta(x' + w')) + \gamma\operatorname{erf}(\beta(x' - w'))) \\ + t'\exp(-2z(x' + w' - \frac{1}{2}z)).[1 + \operatorname{erf}(x' + w' - z)] \\ - t'\exp(-2z(x' - w' - \frac{1}{2}z)).[1 + \operatorname{erf}(x' - w' - z)] \\ - \gamma t'\exp(-2z/\beta)(\beta(x' + w') - \frac{1}{2}z/\beta).[1 + \operatorname{erf}(\beta(x' + w') - z/\beta)] \\ + \gamma t'\exp(-2z/\beta)(\beta(x' - w') - \frac{1}{2}z/\beta).[1 + \operatorname{erf}(\beta(x' - w') - z/\beta)]$$

where the normalized variables:

$$\gamma = g_2/g_1; \beta = \sigma_2/\sigma_1; t' = t/m; x' = x/\sigma_1; w' = w/2\sigma_1; z = \alpha\sigma_1/2v$$

are introduced for simplicity and:

$$\operatorname{erf}(x) = 2\pi^{-\frac{1}{2}} \int_0^x e^{-y^2} dy$$

is the so-called "error function" (MIDDLETON, 1960).

The first four of the eight terms in this expression represent the "maintained" component of the response. The first two terms represent, respectively, the centre "maintained" response to the leading and trailing edges of the figure, and the last two terms, the corresponding responses of the surround. The last four terms of the expression are the analogous "transient" terms of the response. For large values of z each of these "transient" terms approaches a Gaussian curve. For small values of z each of these terms approaches the shape of an exponential curve. These limiting cases agree with the impression that, for small values of v (large values of z) one would expect the response to reflect the shape of the receptive field. Conversely a fast-moving figure is similar to a flashing light and an exponential response term would be expected.

b. *Parameters.* As different units had somewhat different sized receptive fields and firing properties, there are no unique values for the parameters in the above equation. The

parameter values used in the calculated curves to be described were selected as being typical of those found experimentally. They are: $\gamma=4/5$, $\beta=3$, $t'=4$, $\sigma_1=0.59^\circ$, and $\alpha=25/\text{sec}$. They specify a receptive field having a centre 2° in diameter and an overall diameter of about 5° . The strength of the centre response is slightly greater than that of the surround. The amplitude of the transient step response is four times that of the maintained and its time constant of decay is 40 msec.

For $\gamma=0.8$ the total strength of the centre region is slightly greater than that of the surround. The response of a unit to a flashing ambient illumination is thus characteristic of its centre response. This agrees with the experimental findings for most of the units studied (RODIECK and STONE, 1965b). In general, if $\gamma < 1$ then $f(x, y)$ has a maximum surround amplitude much smaller than the maximum centre amplitude. For the parameters above the ratio is 1:20. While such a ratio is needed to permit a centre region to dominate a wider surround, and is further consistent with observations using small moving light spots (RODIECK and STONE, 1965b), it is in apparent conflict with the relative amplitudes of the averaged response histograms to small flashing lights (RODIECK and STONE, 1965b). The ratio of maximum surround response to maximum centre response using small flashing lights was typically about 1:4. Thus while the experimental curves of averaged response amplitudes to flashing light spots are a measure of the general shape of the receptive field, they do not give a direct estimate of the ratio of centre to surround consistent with other observations. This conflict is apparently due to local adaptation effects as the flashing spot measurements were separated in time by up to fifteen minutes (the time needed to record and process the responses at a number of points along a diameter of a receptive field). Thus strong responses would, over a period of minutes, tend to be limited, producing a ratio of maximum surround response amplitude to maximum centre response amplitude more in agreement with the experimental findings.

c. *Calculated curves.* The calculated response of the model unit described above to various sized bars moved at $10^\circ/\text{sec}$ are shown in Fig. 6. The first column shows the bars used, while the second column shows the calculated response curves to these bars. These response curves describe the change in the firing rate of a unit which normally has a

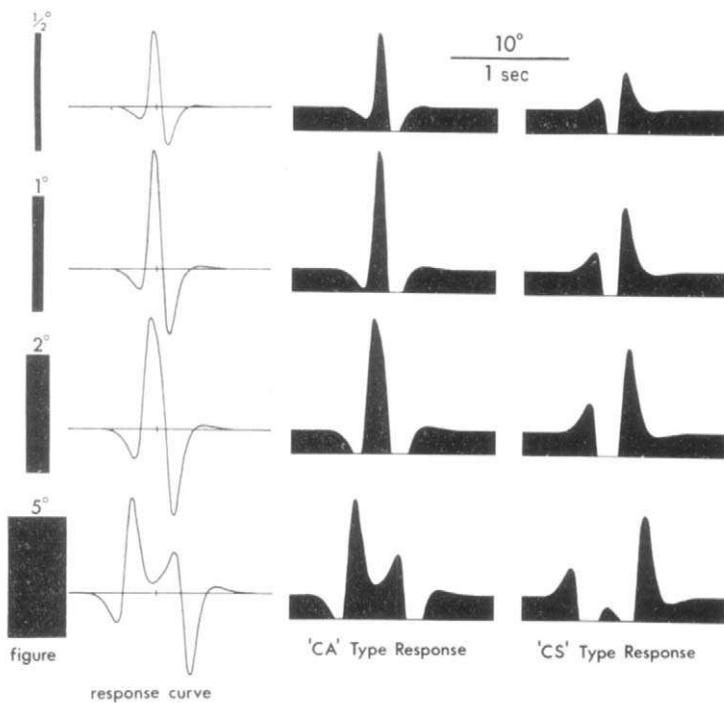


FIG. 6. Calculated response curves for bars of various widths. See text for receptive field parameters used.

maintained firing rate in the absence of stimulation. Thus the "CA" type responses in the third column were drawn by shifting the response curve up by an arbitrary maintained firing level and eliminating that part of the curve which would then correspond to a negative firing rate. The "CS" type responses in the last column were obtained by inverting the response curve and following the same procedure. A vertical scale is not included because, as noted earlier, the adaptation of the retina during the presentation of the flashing light prevents an accurate estimation of this parameter. These calculated response curves should be compared with the experimentally obtained averaged response histograms to the movement of these figures at the same velocity in Figs. 1, 2, 3, 4, 5 and 7 of RODIECK and STONE's first paper (1965a).

Despite the simplified model used to make these calculations, the calculated response curves compare well with those obtained experimentally. Each of the properties of the averaged response histograms listed in Table 1 of that paper are seen also in the calculated response curves. Further similarities are also apparent. In particular, both the calculated and experimental "CA" type responses have peak firing rates for bars having widths of 1-2° which are greater than the peak firing rates for narrower or wider bars.

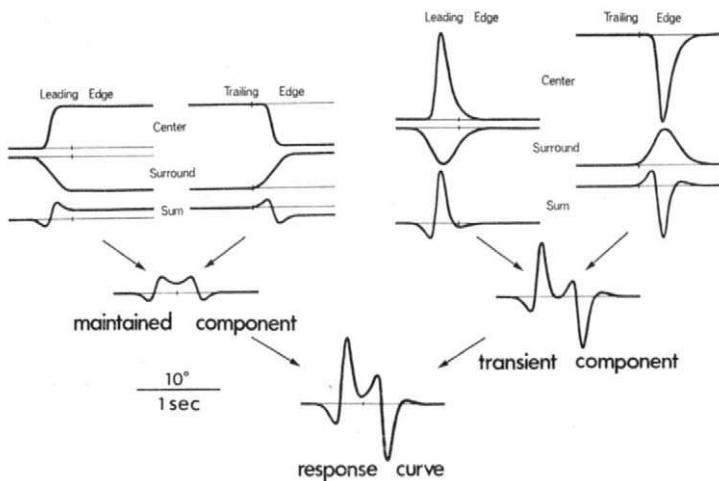


FIG. 7. Illustration of the manner in which the eight terms of the response equation for the 5° bar contribute to the response curve.

d. *Decomposition of the response curves.* It is of interest to consider the manner in which each of the terms in the equation for the response curve contribute to its shape. The response to the 5° bar will be considered because of its relative complexity. In Fig. 7 the maintained and transient components are combined from their individual terms. All of the four terms of the maintained components are similar in shape. They differ only in scaling and position. It is these differences which determine the maintained component. Similar statements apply as well to the terms of the transient component. The division of the response curve into maintained and transient components is not the only possible division. Two other possibilities are: division into centre and surround components, and division into leading and trailing edge components. These three possible divisions are shown in Fig. 8 for the 5° response curve. Inspection of these curves permits easy identification of the generating mechanisms of different parts of the response curves. Thus, for these parameters, the initial peak of the centre activation is seen to be primarily due to the transient centre response of

the leading edge, whereas the second peak is primarily due to the transient surround response of the trailing edge.

The small activation following the complete suppression in the "CA" type response curves is seen to depend critically on the relative amplitudes of the centre and surround response components. This is reflected in the experimental finding that this activation was not observed in all the units studied. The calculated centre response is the expected response curve if a unit either does not have a surround, or has lost its surround during dark adaptation (BARLOW *et al.*, 1957). Comparison of this calculated curve with the comparable experimental findings (Fig. 7, RODIECK and STONE, 1965a) again reveals a good agreement between theory and experiment.

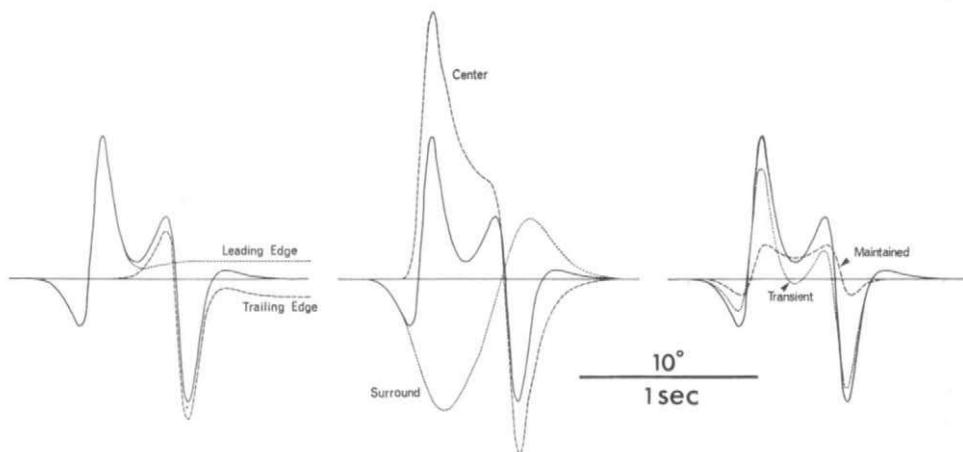


FIG. 8. Three decompositions of the response curve to the 5° bar.

Moving figures of arbitrary shape

As pointed out earlier, moving rectangular figures are particularly simple visual stimuli. A closed form solution for $R(x)$ is easily obtained and each term of the solution has a simple interpretation in terms of receptive field and stimulus parameters. For more complicated stimuli, such as moving discs, a closed form solution does not appear to exist and numerical methods must be employed. It is desirable to choose a method of solution which provides some insight into the coding properties of the retina. The "Green's function technique" (MORSE and FESHBACH, 1953) is such an approach.

Consider the movement of a "point" of light across a receptive field. The point is imagined to have no dimensions in space and is thus completely specified by its position and intensity. The response of an idealized receptive field to this stimulus is:

$$\begin{aligned} G(x, y) = & \frac{1}{2}mg_1(\pi^{-\frac{1}{2}}\sigma_1^{-1}\exp(-y^2/\sigma_1^2)) \\ & [2(1+t')\pi^{-\frac{1}{2}}\sigma_1^{-1}\exp(-(x')^2 - \alpha t'/v)\exp(-2z(x' - \frac{1}{2}z))(1 + \text{erf}(x' - z))] \\ & - \frac{1}{2}mg_2(\pi^{-\frac{1}{2}}\sigma_2^{-1}\exp(-y^2/\sigma_2^2)) \\ & [2(1+t')\pi^{-\frac{1}{2}}\sigma_2^{-1}\exp(-(\beta x')^2 - \alpha t'/v)\exp(-2z/\beta)(\beta x' - \frac{1}{2}z/\beta))(1 + \text{erf}(\beta x' - z/\beta))] \end{aligned}$$

The first pair of terms represent, respectively, the "centre" maintained and transient component responses and the last pair the "surround" maintained and transient component responses. This spatial response curve is shown in perspective view in Fig. 9. The receptive

field parameters are the same as those in the previous computations, and the speed of the point is $10^\circ/\text{sec}$. This two dimensional plot may be viewed either as the response of a single unit to various chordal movements of the point, or as the wave-shape of activation-suppression sweeping across the retina from all the units of similar properties responding to this stimulus. For this latter possibility the point must be viewed as moving in the direction opposite to that of time.

A feature of $G(x, y)$ as the size of the receptive field is decreased, or the velocity of the figure is increased, is the occurrence of two trailing "shoulders" for paths of movement which pass principally through the surround. Similar "shoulders" are therefore to be expected from the response of a unit having a small receptive field to the chordal movement of a small figure. This is, in fact, the experimental finding (fig. 6, RODIECK and STONE, 1965b).

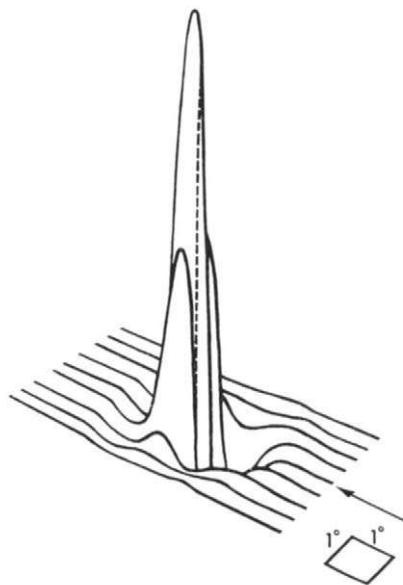


FIG. 9. Perspective view of Green's function for point moving at $10^\circ/\text{sec}$. The position of the point is indicated by the vertical dashed line in the centre curve. The receptive field parameters are the same as those used to calculate the response to moving bars in Fig. 6.

Oscillating spot of light

RODIECK and STONE (1965b) investigated the response of a retinal ganglion cell to a very small ($2'-4'$) spot of light moving back and forth over a small ($\geq 0.5'$) distance within its receptive field. These findings may be briefly summarized by stating that the activation of the cell appeared to be proportional to the gradient of the shape of the receptive field over the path of the spot. In addition the averaged response histogram revealed characteristic properties of the shape of the averaged response in different parts of the receptive field. As might be anticipated the shapes of these averaged response histograms were quite different from the shapes of the responses to either moving figures or flashing lights. The calculated response to this stimulus is thus a third means of testing the validity of the model. The calculated response curves to this stimulus moving in a radial direction over $\frac{1}{2}^\circ$ at

different points in the receptive field of an OFF-centre unit are shown in Fig. 10. The receptive field parameters are the same as those used to calculate the responses to moving figures (Figs. 6 and 7) and the chordal movement of a point source of light through a receptive field (Fig. 9).

Because the moving light spot remained inside the receptive field for a period of minutes rather than passing through it in a few seconds, the maintained firing level, from response to response, depended on the state of light adaptation (see next section). For this reason the

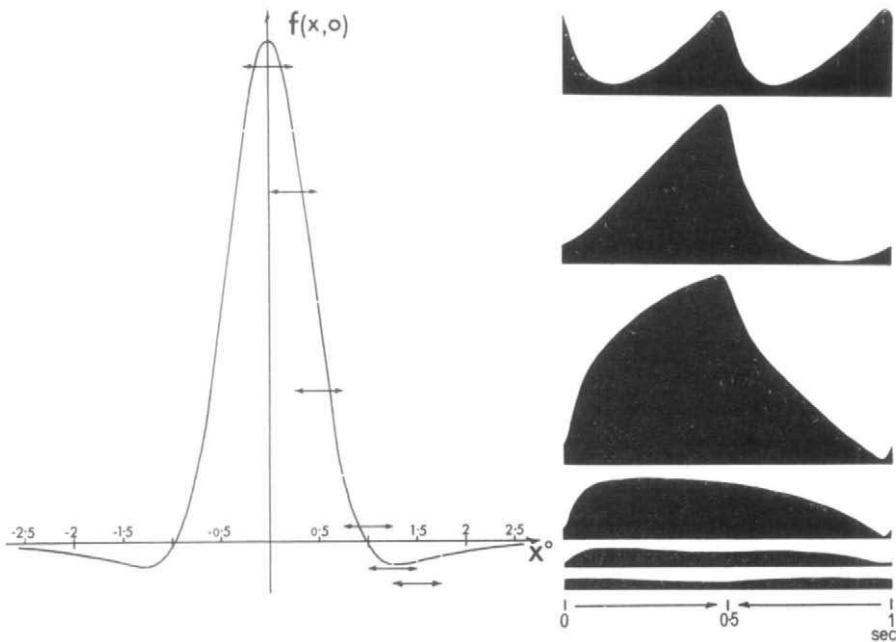


FIG. 10. Calculated responses of OFF-centre unit to a small spot of light moving back and forth in its receptive field over a distance of $\frac{1}{2}^\circ$. The receptive field parameters are the same as those used to calculate the responses in Figs. 6 and 9. The arrows on the receptive field cross-section on the left indicate the paths of movement of the spot for the responses shown on the right.

change in the firing rate is shown in this figure superimposed on a maintained firing level which was selected to facilitate comparison of these calculated curves with the equivalent experimentally obtained response curves (fig. 6, RODIECK and STONE, 1965b). Comparison of the calculated and experimentally obtained curves reveals a relatively good agreement between them thus lending further support to the general validity of retinal superposition. Note particularly the very weak "reversed" response when the spot moved on the outer slope of the surround. This is in agreement with the experimental finding that it was difficult to detect a response to this stimulus moved in this region of a receptive field, but, if one was detected, its direction for activation was "reversed".

Limitations

There are two principal limitations of this quantitative description which prevent its extension to some classes of visual stimuli.

a. *Stimuli of very long duration.* The stimuli used by Rodieck and Stone had durations of about a second. For these stimuli there is a good correlation between experimental and calculated values. Stimuli having durations of the order of minutes or longer, however, cannot be described by the model because of the adaptation taking place during this period. What we describe as a maintained step change in firing rate to a step change in illumination may, in time, return to the previous firing rate (KUFFLER *et al.*, 1957). For this reason, the "maintained component" is, strictly speaking, a "quasi-maintained component" in that its rate of change is considerably slower than the rate of change of the transient component. For stimuli of long duration it is therefore necessary to consider the effect of this "quasi-maintained" component of the response.

b. *Stimuli of very short duration.* The second limitation arises for stimuli having durations significantly shorter than a second. A light flashed for a millisecond is an example. The nature of this limitation is quite different from that described for stimuli of long duration. It was stated earlier that the analytic expressions selected for $h(t)$ and $f(x, y)$ were not critical and that other expressions having approximately the same shapes would serve equally well. This may appear surprising, considering the good correlation between the experimental and calculated values. The explanation lies in the nature of the equation for the response curve, which convolves these analytic expressions. If the expressions are of comparable extent the operation of convolution may be likened to one of "smoothing". This implies that the exact shapes of the analytic expressions are of minor importance compared to their general shapes. Sharp changes and discontinuities in the analytic expressions will be smoothed out. Thus the expression for $h(t)$, although possessing a physically impossible step change in firing rate of zero latency, is adequate for the calculation of the responses of these units either to moving figures or the other visual stimuli used. For the same reason ON-OFF responses (RODIECK and STONE, 1965b) will be smoothed out and have therefore been ignored in these calculations. For stimuli of short duration, however, the convolution integral does not have this smoothing effect, and the response depends critically on the analytic expressions used. Because of the observed variability of firing patterns both from unit to unit, and within the receptive field of a single unit, extension of this quantitative description to the domain of very short stimulus durations requires a thorough investigation of the firing properties of each unit in question.

The model is further limited to the domain of stimulus parameters over which superposition holds. The limits of this domain are presently unknown; however, very bright stimuli which maximally activate a unit undoubtedly lie outside it. The advantage of the analytic expressions selected is that they are mathematically simple and adequate for calculation of responses to many visual stimuli of physiological interest. It should, however, be noted that the quantitative description presented is based on data obtained from paralysed and decerebrate animals. Eye movements are therefore not considered but undoubtedly play an important role in the retinal coding of visual information in the normal animal. If centrifugal fibres to the retina exist, their effect must also be considered.

Deviation from linearity

We have assumed that the sum of the response components is linearly related to the firing rate of a unit. This relation is illustrated as a straight line marked "linear" in Fig. 11. Curves "A" and "B" show the simplest two possible non-linear relationships. To the extent that the relationship between summed response components and firing rate is non-linear the linear curve may be viewed as a first order approximation. A second order approximation

to this relationship would be a curve having the form of either "A" or "B". Inspection of the response histograms illustrated previously reveals a discernible non-linearity in this relation which is of type "A" rather than type "B". The linear relationship implies that it should be possible to invert a "CA" type averaged response histogram and "fit it into" the corresponding "CS" type averaged response histogram. To a first order approximation this is true. In most cases, however, a close fit requires either the activation to be decreased somewhat, or the suppression increased, or a combination of both. Comparison with the calculated curves indicates that the latter situation is the one which brings the calculated curves into best agreement with the experimental findings. Thus the relationship is slightly non-linear. The linear relationship is a good first order approximation and the second order approximation must have a form of type "A" rather than type "B".

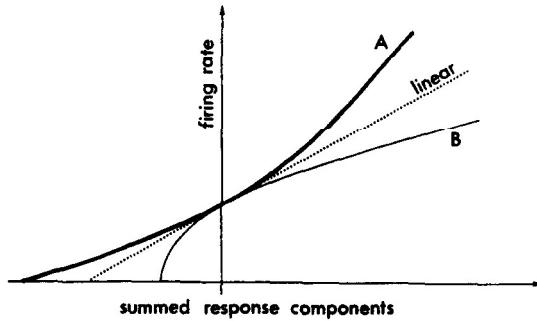


FIG. 11. Two possible second order approximations to the relationship between summed response components and firing rate.

IV. DISCUSSION

Information present in the response curve about movement

If we refer to a spatial response curve like that shown in Fig. 9 as a "wave", then the information available about the movement of a figure is contained both in the wave velocity and the wave shape. (We tacitly exclude movement information obtained from the displacement of an object over long periods of time, e.g. the means by which the movement of the hour hand of a watch, or the tides, are recognized.) The wave velocity is a self-evident factor and, in itself, contains all the movement information contained in the wave shape. The use of the wave shape itself to convey movement information, however, should not be excluded. There are two major changes in the wave shape as the velocity of the figure is increased. The first, for large figures, is a relative increase in the amplitude of the response to the leading edge over the response to the trailing edge for the "CA" type response and the converse for the "CS" type response. The second is a spatial lengthening of the tail of the wave shape. This extension of the tail is suggested in the manner in which cartoonists commonly create the illusion of movement by drawing a number of lines behind an object which is supposed to be moving.

Retinal coding of visual information

The retina acts as a transducer, converting the brightness of the spatial retinal image into a spatial response curve of firing rates of retinal ganglion cells. The positive half of this spatial response curve is encoded primarily by ON-centre units, while the negative half is

encoded primarily by OFF-centre units. The cat's visual perception is based solely on the fidelity with which this response curve is encoded for transmission, via the optic nerve, to the brain.

It is a property of a linear system (i.e. a mechanism in which superposition holds) that if its output (response) is known exactly, then its input can be accurately reconstructed. This implies that if the brain received an exact linear transform of the retinal image then it would be possible, in principle, for it to reconstruct the retinal image exactly. This is generally true so long as there is a monotonic relationship between the spatial response curve and the linear transform of the retinal image. There are two main factors which degrade the accuracy with which the spatial response curve is able to represent the linear transform of the retinal image. Briefly stated, they are the finiteness of the number of cells and the finiteness of their firing rates.

It is convenient to imagine retinal ganglion cells responding not to the retinal image itself but to its linear transform. This simplifies the situation somewhat in that each cell now responds only to the amplitude of the linear transform at the centre of its receptive field. The brain "sees" not the continuous linear transform, but a large number of discrete messages, each supplying rate modulated information about the linear transform. The actual response curve may be viewed as a plane from which arise vertical lines over the centres of the receptive fields. The lines of ON-centre units are above the plane, and those of OFF-centre units below the plane. The amplitude of a line is proportional to the rate of firing of the unit it represents. From this spatial response curve (the encoded message) the brain must decode, as best it can, the inferred linear transform and from it the retinal image.

As retinal ganglion cells fire statistically in time, there is some uncertainty in their responses, which contributes to a loss of information about the linear transform. This may be likened to contributing a random "noise" component to the linear transform. The finiteness of the number of ganglion cells may be likened to "sampling" the linear transform, and results in a further decrement in the information the brain receives about the linear transform.

Relationship to experimental psychology

a. *Approach.* In order to ascribe a retinal origin to some finding in experimental psychology one must determine whether the relevant information is encoded by the retina. Thus the relevant information must actually be lost at the retinal level; the shape of the encoded spatial response curve is irrelevant. For example, the demonstration by OGAWA *et al.* (1965) that a retinal ganglion cell produces the same response either for a very fast flashing light, or a steady illumination, is sufficient to ascribe the origin of the flicker-fusion effect to the retina. Conversely, in human vision, if a moving visual pattern is stopped the pattern often appears to move in the opposite direction for a few seconds (BORING, 1942; BOWDITCH and HALL, 1882). The information provided by the cat's retina is sufficient to prevent such a confusion so that this illusion, if present in the cat, must arise at a higher level in its visual system.

b. *Mach's bands.* It is far more difficult to ascribe a retinal origin to other findings of experimental psychology, even those commonly thought to arise at this level. Thus consider the illusion known as Mach's bands (MACH, 1865, 1914) where at a black and white border the black near the border appears blacker than the rest of the black, and the white near the border appears whiter than the rest of the white. A similar shaped edge effect is seen in the response curves previously described for wide bars. Analogous response curves, observed

by RATLIFF and HARTLINE (1959) for the ommatidia of the *Limulus* eye and by BÉKÉSY (1960) for tactile sensation, led these authors to identify these findings with the phenomenon of Mach bands. This interpretation, although most likely the correct one, incorrectly suggests that sensation is a direct reflection of the encoded spatial retinal response curve. Our subjective impression of the visual world corresponds far more closely to the relative light intensities of the retinal image than to the shape of the spatial response curves described here. In other words, the information transmitted by the optic nerve is encoded information which must be decoded by the brain. To demonstrate that the Mach phenomenon is of retinal origin one must show not that the retinal response curve has a similar shape but that there has been an actual loss of information near this border. Equivalently, one must demonstrate that there is a greater amount of information about intensity present at a fast firing rate than at a slower one. While a burst of firing is a rare event, and thus seemingly has more inherent information, the relevant question is one of variability of firing pattern from response to response, and this study has not as yet been done.

c. *Apparent movement.* There is extensive literature in experimental psychology on so-called "apparent movement" (AARONS, 1964; BORING, 1942). The sensation of visual movement is created if some visual pattern is presented for a short period of time at one point in the visual field and is then presented some milliseconds later at a new position. The appearance of movement in a motion picture is a familiar example of a similar phenomenon. Some experiments have suggested that this phenomenon arises at the retinal level while others (especially binocular studies) ascribe to it a more central origin. It is interesting to consider whether the present study can be related to these psychological findings.

If the phenomenon of apparent movement is of retinal origin it must be shown that two lights flashed successively produce the same shaped response curve in time as does a light turned on, moved a distance, and then turned off. It is not difficult to show that this is, at least approximately, the case. Superposition allows us to consider the response to each light separately. As a light is turned on, the spatial response curve may be envisaged to be a triphasic shape arising quickly to some level, and then more slowly decreasing in amplitude towards another level until the light is turned off, at which time it overshoots (reverses) and finally decays in amplitude to zero. If the lights are separated by an angular distance sufficiently smaller than a receptive field then it is easily seen that the introduction of the second light causes an effective movement of the peak of the total spatial response curve towards the second light. This is, however, exactly the time course and shape to be expected from the stimulus of a light turned on, moved and turned off. Thus, to the extent that these two spatial response curves are the same, the brain will be unable to distinguish between them and the phenomenon demonstrated to have a retinal origin.

SUMMARY

1. This paper concludes a series of three papers on the response of cat's retinal ganglion cells to visual stimuli.
2. The concept of superposition has been found to be a useful and powerful one to apply to retinal function. It demonstrates a close relationship between certain properties of the receptive fields of retinal ganglion cells and their response to visual stimuli. An equation which enables calculations of these responses to a wide range of visual stimuli is derived.
3. Calculated responses are presented for moving rectangular bars, chordal movement of small figures, and small oscillations of a spot of light. These calculated responses agree

well with the experimentally obtained averaged response histograms described in the previous two papers.

4. Retinal coding of visual information is discussed and related to some findings from experimental psychology.

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Abstract—The concept of superposition has been found to be a useful and powerful one to apply to retinal function. It demonstrates a close relationship between certain properties of the receptive field of a retinal ganglion cell and its response to visual stimuli. An equation which enables calculations of responses to a wide range of visual stimuli is derived. Calculated responses are presented for moving rectangular bars, chordal movement of small figures, and small oscillations of a spot of light. These calculated responses agree well with experimental data. Retinal coding of visual information is discussed and related to some findings from experimental psychology.

Résumé—On montre l'utilité et la richesse du concept de superposition appliquée aux fonctions rétinianes. Il permet de démontrer une étroite relation entre certaines propriétés du champ récepteur d'une cellule ganglionnaire rétinienne et sa réponse aux stimuli visuels. On établit une équation qui permet de calculer les réponses pour une grande variété de stimuli visuels. On présente les réponses calculées pour des barres rectangulaires en mouvement, le va-et-vient de petites figures, et les faibles oscillations d'un point lumineux. Ces réponses calculées s'accordent bien avec les données expérimentales. On discute le codage rétinien de l'information visuelle, en relation avec certains résultats de psychologie expérimentale.

Zusammenfassung—Die Anwendung des Superpositionsprinzips auf retinale Funktionen erwies sich als brauchbar und treffend. Es zeigt eine enge Beziehung zwischen gewissen Eigenschaften des rezeptiven Feldes einer retinalen Ganglienzelle und ihrer Antwort auf visuelle Reize. Es wird eine Gleichung abgeleitet, die es ermöglicht, Antworten für viele visuelle Reize zu berechnen. Die berechneten Antworten werden gezeigt für bewegte rechteckige Streifen, geradlinige Bewegungen kleiner Figuren und kleine Schwingungen eines Lichtpunktes. Diese berechneten Antworten stimmen gut mit den experimentellen Daten überein. Die retinale Codierung der visuellen Information wird diskutiert und zu einigen Ergebnissen der Experimentalpsychologie in Beziehung gesetzt.

Резюме—Понятие суперпозиции оказалось полезным в приложении к функции сетчатки. Продемонстрированы тесные взаимоотношения между определенными свойствами рецептивного поля ганглиозной клетки сетчатки и ее реакцией на световые стимулы. Выведено уравнение, которое позволяет расчитать реакции в широком диапазоне световых стимулов. Вычисленные реакции представлены: для движущихся четырехугольных полосок, хордального движения малых фигур и малых осцилляций светового пятна. Эти расчетные реакции находятся в хорошем согласии с экспериментальными данными. Обсуждается ретинальное кодирование зрительной информации и сопоставляется с некоторыми данными экспериментальной психологии.