THE RESPONSES OF LIMULUS OPTIC NERVE FIBERS TO PATTERNS OF ILLUMINATION ON THE RECEPTOR MOSAIC*

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ABSTRACT

The inhibition that is exerted mutually among receptor units (ommatidia) of the compound eye of *Limulus* is less for units widely separated than for those close together. This diminution of inhibition with distance is the resultant of two factors: (1) the threshold of inhibitory action *increases* with increasing distance between the units involved; and (2) the coefficient of inhibitory action *decreases* with increasing distance.

The discharge of nerve impulses from ommatidia at various distances from one another may be described quantitatively by a set of simultaneous linear equations which express the excitatory effects of the illumination on each ommatidium and the inhibitory interactions between each ommatidium and its neighbors. The values of the thresholds and coefficients of inhibitory action, which appear as parameters in these equations, must be determined empirically: their dependence on distance is somewhat irregular and cannot yet be expressed in an exact general law. Nevertheless the diminution of inhibitory influences with distance is sufficiently uniform that patterns of neural response generated by various patterns of illumination on the receptor mosaic can be predicted qualitatively. Such predictions have been verified experimentally for two simple patterns of illumination: an abrupt step in intensity, and a simple gradient between two levels of intensity (the so-called Mach pattern). In each case, transitions in the pattern of illumination are accentuated in the corresponding pattern of neural response.

One of the significant features of the pattern of stimulation on the receptor mosaic of a sense organ is the locus of transitions from one level of intensity to another. Such transitions may be accentuated, in the patterns of neural activity generated by the sense organ, by neural interaction among the receptor units which make up the receptor mosaic. For example, in the lateral eye of *Limulus* the receptor units (ommatidia) are interdependent: the discharge of impulses

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from any one of them depends not only upon the stimulus to it, but also upon the activity of its neighbors. This interaction is purely inhibitory and is exerted mutually among the receptor units; each inhibits its neighbors and is, in turn, inhibited by them. The response of a receptor unit in the lateral eye of *Limulus* is most effectively inhibited by the illumination of other receptor units close to it; the effectiveness diminishes with increasing distance, although it may extend for several millimeters (Hartline, Wagner, and Ratliff, 1956). As we have briefly reported (Ratliff and Hartline, 1957; and Ratliff, Miller, and Hartline, 1958), the greater the separation between units, the higher are the thresholds and the smaller the inhibitory coefficients of their mutual interaction. It is the purpose of the present paper to describe, in detail, this dependence of the inhibitory action on distance and to demonstrate by experiment some of its consequences for pattern vision.

METHOD

The experiments to be reported are based on the measurement of the frequency of the discharge of nerve impulses in single optic nerve fibers. In each experiment, a lateral eye of an adult *Limulus* was excised with 1 to 2 cm. of optic nerve and mounted in a moist chamber maintained at 17.5°C. Small strands separated from the optic nerve were dissected until only a single active fiber remained in each, as evidenced by the uniformity and regularity of the action potential spikes observed and by the fact that they could be elicited only by illumination of a particular receptor unit (ommatidium). Each such small strand could be placed on a separate pair of wick electrodes connected to its own separate amplifying and recording system. In most of the experiments the frequencies of discharge of impulses in optic nerve fibers from two receptor units, or in some cases three, were measured simultaneously. In a few experiments we observed the discharge from a single receptor unit in response to some pattern of illumination, of a fixed configuration, in various positions on the receptor mosaic. Details of our method have been given in previous papers (Hartline, Wagner, and Ratliff, 1956; Hartline and Ratliff, 1957; and Hartline and Ratliff, 1958). As in those papers, we have confined our attention to the frequency of discharge of impulses that is maintained at a more or less steady level during steady illumination of the eye; the transient changes in frequency that occur during the first second or two after light is turned on or off were excluded from the measurements.

A typical measurement of the inhibitory effect was made as follows. A test receptor was illuminated alone at some fixed intensity for a period of 12 seconds. Beginning 3 seconds after the onset of this illumination the impulses discharged during the next 8 seconds were counted. After a 2 minute interval of rest, to minimize cumulative effects of light adaptation, the test receptor was again illuminated, together with a small group of adjacent receptor units, for 12 seconds. The activity of one of these adjacent units was recorded as representative of the activity of that group. As before, 3 seconds after the onset of illumination the impulses discharged from the test receptor were counted for a period of 8 seconds; simultaneously, the impulses discharged from the receptor in the adjacent group were counted separately. Two minutes later the

test receptor was illuminated alone and the impulses discharged from it were counted, again for a period of 8 seconds. The frequency of impulses discharged by the test receptor when it and the neighboring group were illuminated together was substracted from the average of the two frequencies determined when the test receptor was illuminated alone. This difference was taken as the measure of the magnitude of the inhibition exerted upon the test receptor by the neighboring group of receptors. Modifications of this general technique, to suit particular experimental requirements, are described below.

RESULTS

We have analyzed the dependence of the inhibitory action on distance by measuring the inhibition exerted by a small group of receptors on two other receptor units located at different distances from it. The frequency of the discharge of impulses by one of the receptors in this small group (A) was taken as a measure of the level of activity of the whole group, and—in terms of this measure—the threshold and the inhibitory coefficient of the action of this group on the other two receptors (B and C) were determined.

The results of such an experiment are shown in Fig. 1. At low frequencies of discharge, the group of ommatidia (A) exerted no effect on either ommatidium B or ommatidium C. At successively higher frequencies of discharge from the group A, produced by higher intensities of illumination upon it, the threshold of its inhibitory effect on the nearest ommatidium (B) was reached (at 5.1 impulses/sec.), and the magnitude of the effect on this nearby element then increased with a large coefficient (0.17 impulse/sec. decrease in the discharge of B per impulse/sec. discharged in A). The threshold of the effect on the more distant ommatidium (C) was not reached until the frequency of discharge of A was much greater (18 impulses/sec.) and when reached it then increased with a much smaller coefficient (0.07) than did the effect on the nearer ommatidium (B).

Similar results have been obtained in a number of similar experiments, and—as a general rule—we have found that the threshold increases and that the inhibitory coefficient decreases with increasing distance between the unit inhibited and the unit or units inhibiting it. We have found, however, some minor exceptions to this rule. Occasionally the threshold of action was larger, and the inhibitory coefficient smaller, for a nearer element than for a more distant one. Such inversions are not observed when the difference in distance is very great, but they are sufficiently large and occur often enough so that it is apparent that any law relating magnitude of inhibition to distance must be of a statistical nature (see Discussion).

In the above experiment only the inhibitory action of one particular group of receptors (A) on two other receptors (B and C) at different distances from it was determined. In the following experiments we determined the effects of a

number of different groups (A_1, A_2, etc.) on two such receptors (B and C) in various spatial configurations. Since it is not an easy technical matter to record from optic nerve fibers arising from each of these several groups we recorded from only the two receptors B and C and compared the effects exerted simul-

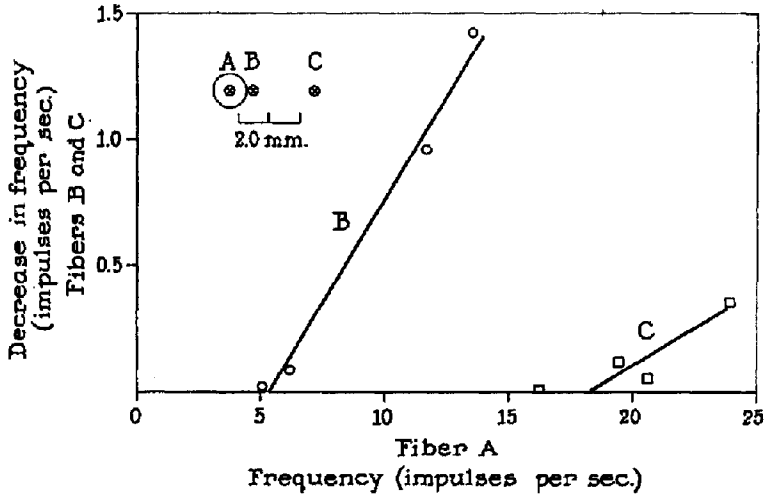

FIG. 1. The dependence of the magnitude of inhibition on distance. The inhibition (measured in terms of decrease in frequency) exerted by a small group of receptors (A) on two other receptors (B and C) is plotted as ordinate. As abscissa is plotted the concurrent frequency of the discharge of impulses of one of the receptors in the group A. The geometrical configuration of the pattern of illumination on the eye is shown in the insert. The locations of the facets of the receptors whose discharges were recorded are indicated by the symbol ⊗. The receptor A was at the center of a group of six or seven receptors illuminated by a spot of light 1 mm. in diameter. The illumination B and C was provided by spots of light 0.2 mm. in diameter and of fixed intensity. Measurements were made as described in the section on Method. The effects of the group A on B and on C were determined separately. Each point on the graph B is the average of three separate determinations; the points on the graph C are averages of from two to five separate determinations.

taneously on them by each of the several groups (A_1, A_2, etc.) in succession. It was possible, by this means, to determine the *relative* magnitudes of the inhibitory effects exerted on the two receptors by other groups of receptors at various distances from them without actually measuring the levels of activity of these groups of receptors.

The results of one such experiment are shown in Fig. 2. The group of receptors A_1, located equidistant from the receptor units B and C, exerted equal inhibitory effects on both. The group of receptors in the position A_2, closer to B than to C,

exerted larger effects on B than on C. Although the responses of B and C were measured simultaneously, the conditions were such that they did not inhibit one another appreciably (tested by a separate experiment).

The results of a similar but more extensive experiment are shown in Fig. 3. The group of receptors, A_2, symmetrically located with respect to receptor units B and C, exerted nearly equal simultaneous effects upon them. The

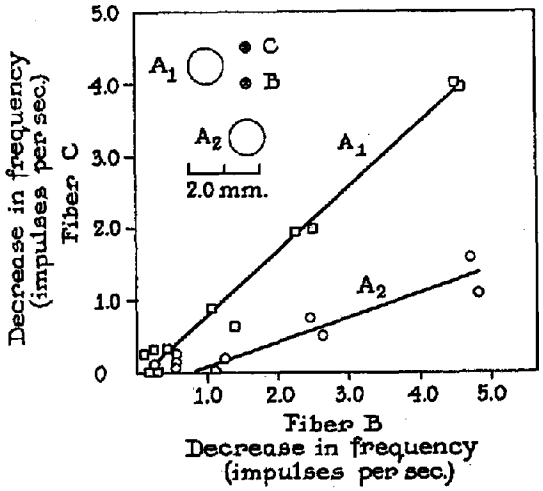

FIG. 2. The relative magnitudes of inhibition exerted on two receptors by a group of receptors equidistant from them, and by another group nearer to one than to the other. Records were obtained of the discharge of impulses from two receptors B and C, elicited by small spots of light 0.2 mm. in diameter and of fixed intensity confined to their facets. A third spot of light 1 mm. in diameter could be placed in either of two positions (A_1 or A_2) relative to B and C, as shown in the insert. In each of these positions the inhibitory effects exerted on B and C were determined simultaneously at various levels of intensity of A. For each point the decrease in the frequency of discharge of B is plotted as abscissa; the simultaneous decrease in frequency of discharge of C is plotted as ordinate.

group A_3, located near B_1 exerted a large effect on B and at the same time, practically no effect on C. A_1, on the other hand, was close to C and at a considerable distance from B; correspondingly there was a large inhibitory effect on C, and at the same time, a small effect on B.

The two experiments just described yield no direct information about the relation of the magnitude of the inhibitory effect to the level of activity of the receptor units exerting the inhibitory influence; they do show, however, that the relative magnitudes of the inhibitory effects are not the results of chance differences in the properties of the units that happened to have been chosen as

test receptors. Since the effect on one unit may be changed relative to the effect on the other simply by changing the location of the inhibiting units, it is evident that these differences in the inhibition are attributable to the different distances between the inhibiting units and the test receptors. Consequently, the degree of inhibitory interaction among any set of receptor units in the lateral eye of *Limulus* must be determined, in part, by the locations of these units, relative to one another, in the receptor mosaic.

Theory—In our previous papers (Hartline and Ratliff, 1957, and Hartline and Ratliff, 1958) we showed that the activity of n interacting receptors may be described

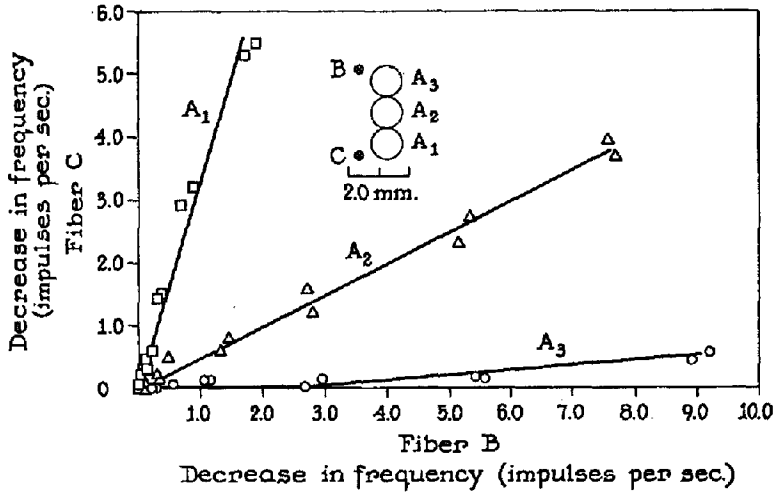

FIG. 3. The relative magnitudes of inhibition exerted on two receptors by other receptors in various positions with respect to them. The decrease in the frequency of discharge of B, for several intensities of A at each of three positions is plotted as abscissa; the simultaneous decrease in frequency of C, at each such position and intensity is plotted as ordinate. Same procedure as for the experiment of Fig. 2.

by a set of simultaneous linear equations, each with $n - 1$ inhibitory terms combined by simple addition:

$$r_p = e_p - \sum_{\substack{j=1 \\ j \neq p}}^{n} K_{pj}(r_j - r^0_{pj}) \qquad \begin{matrix} p = 1, 2 \cdots n \\ j \neq p \end{matrix}$$

The activity of a receptor unit—its response (r)—is measured by the frequency of discharge of impulses in its axon. This response is determined by the excitation (e) supplied by the external stimulus to the receptor, diminished by whatever inhibitory influences may be acting upon the receptor as a result of the activity of neighboring receptors. The excitation of a given receptor is measured by its response when it is illuminated by itself, thus lumping together the physical parameters of the stimulus and the characteristics of the photoexcitatory mechanism of the receptor. In each

such equation, the magnitude of the inhibitory influence is given by the summated terms, written in accordance with the experimental findings as a simple linear expression. The "threshold" frequency that must be exceeded before a receptor can exert any inhibition is represented by r^0. It and the "inhibitory coefficient," K, in each term are labelled to identify the direction of the action: r^0_{pj} is the frequency of receptor j at which it begins to inhibit p; K_{pj} is the coefficient of the inhibitory action of receptor j on receptor p. Restrictions on these equations have been described elsewhere (Hartline and Ratliff, 1958).

The theoretical significance of the experiments reported in this paper is in the finding that the diminution of the inhibitory effect with increasing distance, which we observed earlier (Hartline, Wagner, and Ratliff, 1956), may now be ascribed more exactly to the combined effects of increasing thresholds (r^0_{pj}) and decreasing inhibitory coefficients (K_{pj}) which accompany increasing separation of the interacting elements p and j.

Although we can thus conveniently describe the activity of a system of interacting elements without making explicit reference to their relative locations in the receptor mosaic and to the spatial pattern of illumination (since the dependence of the inhibitory influences on distance is implicit in the values of the thresholds and inhibitory coefficients), it is nevertheless clear that the strong dependence of the inhibitory thresholds and coefficients on the separation of the elements introduces a topographic factor which must give to the inhibitory interaction its special significance in retinal function. Any complete description of the spatial characteristics of the inhibitory interaction must, therefore, provide an explicit statement of the relations between these inhibitory parameters and the corresponding distances on the receptor mosaic. At the present time, however, we are not prepared to state these relations in an exact quantitative form (see Discussion).

On the basis of the diminution of the inhibitory interaction with increasing distance one can predict the general form of the patterns of response which will be elicited from the elements of the receptor mosaic by various spatial patterns of illumination. Contrast effects, for example, may be expected to be greatest at or near the boundary between a dimly illuminated region and a brightly illuminated region of the retina. A unit which is within the dimly illuminated region, but which is near this boundary, will be inhibited not only by dimly illuminated neighbors but also by brightly illuminated ones. The total inhibition exerted on it will therefore be greater than that exerted upon other dimly illuminated elements that are farther from the boundary; consequently its frequency of response will be less than theirs. Similarly, a unit within but near the boundary of the brightly illuminated field will have a higher frequency of discharge than other equally illuminated units which are located well within the bright field but which are subject to stronger inhibition since all their immediate neighbors are also brightly illuminated. Thus the differences in the activity of elements on either side of the boundary will be exaggerated and the discontinuity in this pattern of illumination will be accentuated in the pattern of neural response.

The ideal experimental test of these qualitative predictions would be to record simultaneously the discharge of impulses from a great number of receptor units in many different positions with respect to a fixed pattern of illumination on the receptor mosaic. Such a procedure is impractical, so we measured, instead, the discharge of impulses from only one receptor unit near the center of the eye, and shifted the pattern of illumination between measurements so that this one receptor unit assumed successively a number of different positions with respect to the pattern.

The pattern of illumination was provided by focussing on the eye the demagnified image of a transilluminated photographic plate on which the desired

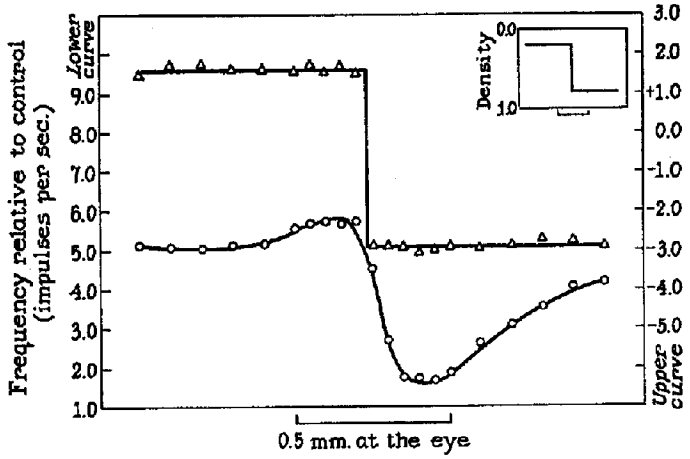

FIG. 4. The discharge of impulses from a single receptor unit in response to a simple "step" pattern of illumination in various positions on the retinal mosaic. The pattern of illumination was rectangular, covering an area 1.65 mm. × 1.65 mm. on the eye. It was obtained by projecting the demagnified image of a photographic plate on the surface of the eye. The insert shows the relative density of the plate along its length as measured, prior to the experiment, by means of a photomultiplier tube in the image plane where the eye was to be placed. The density of the plate was uniform across its entire width at every point. The measurements illustrated were made over the central 1.5 mm. of the image on the eye.

The upper (rectilinear) graph shows the frequency of discharge of the test receptor, when the illumination was occluded from the rest of the eye by a mask with a small aperture, minus the frequency of discharge elicited by a small "control" spot of light of constant intensity also confined to the facet of the test receptor. Scale of ordinate on the right.

The lower (curvilinear) graph is the frequency of discharge from the same test receptor, when the mask was removed and the entire pattern of illumination was projected on the eye in various positions, minus the frequency of discharge elicited

pattern of density had been developed. (This method permits more convenient control of the pattern of stimulation of the receptor mosaic than does the use of real illuminated objects in the visual field.) In the first experiment to be described the plate consisted of two contiguous rectangular areas, one of a uniform high density and the other of a uniform low density. The plate could be moved in a direction perpendicular to the boundary between the two areas, thus its image could be placed in a number of positions on the eye with respect to the ommatidium from which records were being obtained. In one part of the experiment, the entire eye, including the test receptor, was exposed to the pattern of illumination. For comparison, in another part of the same experiment, we exposed the test receptor alone to the same intensities of illumination. To do this, a mask with a small aperture was placed in a fixed position between the movable plate and the eye so that only the light passing through whatever area of the plate was imaged on the test receptor could reach the eye. A second channel of illumination, brought together with the first by means of a combining prism, could provide a second small beam of light of constant intensity, also confined to the facet of this same ommatidium. This provided the stimulus for control measurements with which the two sets of experimental measurements were subsequently compared. (This was necessary because we could not change quickly enough from the masked to the unmasked arrangement to make a direct comparison.)

The stimulus was turned on every 2 minutes for a period of 7.5 seconds. Beginning 2 seconds after the onset of this illumination the nerve impulses

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by a small "control" spot of light of constant intensity confined to the facet of the receptor. Scale of ordinate on the left.

The image on the eye of the fixed aperture in the mask was made much smaller (0.05 mm. in diameter) than the facet of the test receptor (approximately 0.2 mm. in diameter) in order to insure that no light would reach adjacent receptors. Thus the absolute amount of light entering the receptor under this condition was considerably less than when the entire pattern was projected in the same position on the eye and the entire aperture of the test receptor was filled. (Use of the full aperture also produced a certain amount of "smoothing" of the lower curve.) In each case the intensity of the "control" spot of illumination was adjusted to produce a frequency of discharge in approximately the same range as the test measurements. The average control frequency for the upper curve was 12.8 impulses per second; for the lower curve, 9.0 impulses per second. The positions of the graphs on the ordinate were arbitrarily fixed by locating the point on the extreme right of the curvilinear graph one impulse per second below the corresponding point on the rectilinear graph. Such a displacement is in accordance with the common observation that, due to the inhibitory interaction, the frequency of discharge in a single optic nerve fiber is smaller when a large area of the eye is illuminated than when a small spot is used that just fills the entire aperture of that fiber's ommatidium. The principal point of comparison is the *form* of the curves rather than the absolute magnitudes of the frequencies.

discharged during the next 5 seconds were counted. Measurements were made of the discharge in response to the control stimulus of fixed intensity followed 2 minutes later by measurements of the discharge in response to light passing

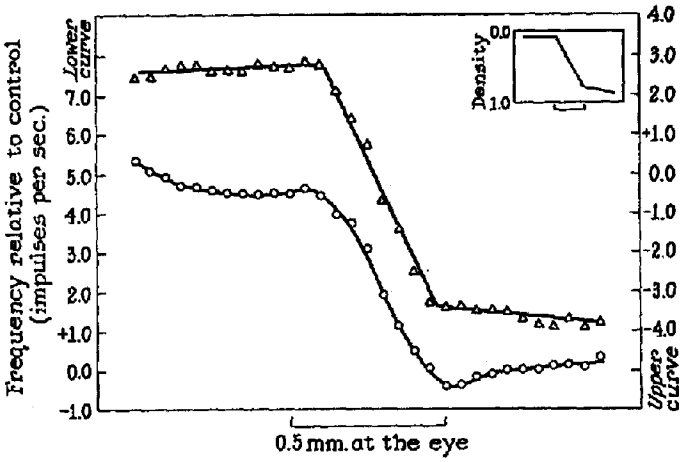

FIG. 5. The discharge of impulses from a single receptor unit in response to a pattern of illumination on the eye containing a simple gradient of intensity. The insert shows the relative density along the length of the photographic plate whose demagnified image (2.0 mm. × 2.0 mm.) was projected on the eye to provide the pattern of illumination. The density of the plate was uniform across its entire width at every point. The measurements illustrated were made over the central 1.5 mm. of the image on the eye.

The upper (rectilinear) graph shows the frequency of discharge of the test receptor, when the illumination was occluded from the rest of the eye, minus the frequency of discharge elicited by a small control spot of light of constant intensity confined to the facet of the test receptor. Scale of ordinate on the right.

The lower (curvilinear) graph is the frequency of discharge from the same test receptor, when the entire pattern was projected on the eye in various positions, minus the frequency of discharge elicited by a small control spot of light of constant intensity confined to the facet of the test receptor. Scale of ordinate on the left. Same procedure as for the experiment of Fig. 4. Average control frequency for the upper curve was 15.2 impulses per second; for the lower curve, 9.0 impulses per second.

through the plate with the mask in place followed again 2 minutes later by another control measurement. Following each such set of measurements the plate was shifted to a new position, with respect to the eye and the mask, at which the next set of measurements was made, and so on. The measurements made with the mask in place, and plotted relative to the control measurements, are analogous to physical measurements which might be made by scanning the plate with a densitometer of small aperture; that is, they show the response of a

single photoreceptor unit to the illumination transmitted through the various portions of the plate. The resulting graph (Fig. 4, upper curve) is a rectilinear one closely resembling the distribution of density on the plate.

Next the mask was removed from the optical system so that the image of the entire plate was projected on the eye, illuminating all of the receptor mosaic in the neighborhood of the test receptor. The plate was again shifted in steps as before so that, in effect, the test receptor and its neighbors "scanned" in successive steps across the image of the plate. Since the response of the receptor unit was not, in this latter case, determined solely by the illumination on it, but also by the activity of the neighboring units, the response was no longer a simple function of the intensity of illumination on that receptor. As predicted above, the transition from the one level of intensity to the other was accentuated, with a maximum and a minimum appearing in the pattern of the response as a result of the inhibitory interaction among the neighboring receptors (Fig. 4, lower curve).

Particularly interesting among contrast phenomena are the dark and light bands seen at the edges of the penumbra of a shadow cast by an object placed in front of an extended source (first studied by Mach, 1865). To duplicate such a pattern in our experiments, a photographic plate was prepared, similar to the one described above, but with a more gradual linear gradation of density between the regions of uniform high and uniform low density. When the pattern of illumination thus obtained was moved across the eye of *Limulus*, utilizing the same general method as in the experiment just described, maxima and minima were found in the response of the test receptor even though there are no such maxima and minima in the distribution of intensity across the eye (Fig. 5). The explanation of this follows the same line of argument as that given above for a sharp step in the intensity.

DISCUSSION

It is evident from the results of the present experiments that each receptor unit exerts a field of inhibitory influence around itself. The extent and the magnitude of the field of inhibitory influence exerted by a particular ommatidium are not fixed, but depend upon the level of activity of that ommatidium. At low levels of activity only the thresholds of inhibitory action on nearby receptor units are reached; at higher levels more distant receptors are affected. Once the thresholds have been reached the magnitude of the inhibition exerted by an ommatidium on others near it increases rapidly with increases in its level of activity, while the inhibition it exerts on more distant ones increases only slowly.

This dependence of inhibition on distance between any two receptors in the mosaic cannot be expressed by simple mathematical functions relating the Ks and r^0s on the one hand to the separation between receptors on the other. One

reason is that the thresholds and coefficients of the interaction between two receptor units are not always identical for both directions of action (Hartline and Ratliff, 1957). Furthermore, the inhibitory influences do not diminish uniformly in all directions from the receptors exerting the influence; they fall off more abruptly in dorso-ventral directions than in antero-posterior directions (Hartline, Wagner, and Ratliff, 1956). Also, in exceptional cases the threshold of action on a more distant element may be smaller, and the inhibitory coefficient greater than for a somewhat nearer element. However, such variability might be expected when the relationships are expressed in terms of direct distances across the surface of the receptor mosaic, for such distances are not necessarily equal to the distances over which the inhibitory influences may actually be transmitted in the plexus of lateral interconnections among the receptors. Such variability is relatively minor and yet it cannot be neglected; the general law relating inhibition to distance will ultimately have to be formulated in statistical terms. At present we do not have a sufficiently large number of measurements covering a wide variety of locations, directions, and distances such as will be required to formulate exactly such a law.

The physiological bases for the diminution of the inhibitory influence with distance are unknown. One possibility is that the effect may diminish with distance simply because of a decrement in transmission over the individual fibers of the plexus of lateral interconnections. Another possibility is that the effect may be transmitted without true decrement in the individual fibers and branchlets of the plexus, but that the magnitude of the total effect exerted on particular receptors may be greater the larger the number of active branchlets of the lateral connections terminating in neuropile around axons of the affected receptor units. Then if the branchlets of the lateral interconnections were more profuse near the units from which they arise than they are some distance away, the magnitude of the inhibition would diminish with distance even though conducted without decrement in the individual fibers. Since we have not, as yet, been able to record electrical activity in these lateral interconnections, nor to trace all their ramifications, any discussion of the matter must be speculative. (For details of the structure of the ommatidium, see Miller, 1957 and 1958; for the structure of the plexus and neuropile, see Ratliff, Miller, and Hartline, 1958.)

The physiological significance of the dependence of the inhibition on distance may be readily understood. Since intensely stimulated receptors exert stronger inhibition on less intensely stimulated ones than the latter exert on the former, and since these effects diminish with distance, contrast will be most strongly enhanced near the borders of differently stimulated regions of the receptor mosaic.

These consequences of inhibitory interaction could, in principle, be derived in exact mathematical form from the set of equations given above, once the

law has been formulated giving the values of the Ks and r^0s as functions of distance between receptors. Until this formulation has been made, however, any mathematical model must remain largely speculative. Nevertheless, any hypothetical law that postulates the Ks decreasing and the r^0s increasing with increasing receptor separation (which experiment shows to be a fact, on the average) will predict, for appropriate intensity distributions similar to those we have used, maxima and minima in the patterns of receptor response that will be like those we have observed in the actual experiments of Figs. 4 and 5. We have investigated a few speculative models in which the inhibition was assumed to decrease with distance according to various laws. The set of simultaneous equations was written to describe the responses of receptors in a mosaic exposed to a step-function distribution of intensity; iterated substitution of successive numerical approximations converged to solutions that showed maxima and minima bordering the intensity step, resembling those in Fig. 4. The spatial distribution of the calculated "responses" did not differ greatly from that yielded by the theoretical model proposed by Fry (1948) to account for Mach's bands in human vision. Fry's postulates do not assume *mutual* inhibition of receptors. A mathematical model postulated by Taylor (1956) also yields maxima and minima of activity bordering a step-transition in intensity of stimulus to a mosaic of neural elements. His model provides for mutual interaction, and is similar to the one we have found by experiment to describe interaction in the *Limulus* eye. It differs in making no provision for varying thresholds of the inhibitory action, and the cases considered did not include graded inhibitory coefficients. These exercises are instructive, but it would be premature to try to fit the experimental data of this paper by a quantitative theory at the present time.

In human vision the pronounced brightness contrast near borders, the marked bright and dark lines known as Mach's bands (Mach, 1865), and the differing depressions of visual thresholds by adjacent illumination at different distances (Beitel, 1936) may all be explained by postulating such inhibitory influences in the visual pathways which decrease with distance (Fry, 1948). In addition to these "first order" effects, the phenomenon of *disinhibition* which we reported earlier (Hartline and Ratliff, 1957) also has its explanation in the dependence of the inhibitory effect on distance. Receptor units too far from another to affect it directly may nevertheless exert an indirect influence on it by inhibiting the activity of other intermediate receptors which do exert direct inhibitory influences upon it. Whether the disinhibition we have observed in the lateral eye of *Limulus* has a counterpart in human vision is not known. It seems probable that since some inhibitory effects in the human eye do diminish with distance the proper experimental arrangement might reveal disinhibition as well. It is also probable that various features of the organization of receptive fields in the vertebrate eye (Hartline, 1940; Kuffler, 1953; Barlow, 1953; Barlow,

FitzHugh, and Kuffler, 1957) are partly brought about by inhibitory influences which diminish with distance.

Similar inhibitory mechanisms are undoubtedly important in other sensory systems. For example, the possible role of inhibitory interaction as a "sharpening" mechanism in the auditory system was pointed out many years ago (Békésy, 1928); and, more recently, such inhibition has actually been observed in the auditory pathways (Galambos and Davis, 1944). In addition, contrast effects—similar to Mach's bands in vision—have been observed in skin sensations (Békésy, 1958).

In every instance cited it appears that the strong dependence of the inhibitory interaction on the separation of the elements in the receptor mosaic introduces a topographic factor which gives the inhibition its special significance in sensory function. As a consequence of this dependence, certain features of the spatial pattern of stimulation are enhanced in the pattern of sensory nerve response at the expense of accuracy of less significant information about intensity of stimulation on each receptor.

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