Inhibitory Fields in the *Limulus* Lateral Eye

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ABSTRACT The inhibition that is exerted mutually among receptor units (ommatidia) of the lateral eye of *Limulus* does not diminish uniformly with increasing distance between units. Instead the response of a receptor unit is most effectively inhibited by other units separated from it by approximately 1 mm (three to five receptor diameters); the effectiveness diminishes with distances both greater and less than this value. The ommatidial inhibitory field as measured by the spatial function of the inhibitory coefficients contains a uniform depression in the central region, a uniformly high annulus at some distance from the center, and a gradual tapering off toward the periphery. The field is large—covering over 30% of the retina—and is somewhat elliptical in shape with its major axis in the anteroposterior direction on the lateral eye. A number of experiments reveal similar configurations in a sizable part of the eye. Control experiments show that the diminution of the inhibitory effects near the center of the field is not an artifact of the measuring technique and cannot be explained readily by local neural excitatory processes.

INTRODUCTION

Over a century ago, Ernst Mach (1865) investigated the well-known ability of the visual system to accentuate contrast at borders and at steep intensity gradients in the retinal image. With remarkable insight he concluded that this accentuation must arise from a reciprocal inhibitory interaction of neighboring retinal elements, and that the interaction must diminish with increasing separation of the elements. Physiological evidence to support Mach's conclusion was provided by Hartline, Wagner, and Ratliff (1956) who found that the response of a receptor unit (ommatidium) in the lateral eye of *Limulus* is inhibited by illuminating other receptor units close to it; the effectiveness diminishing with increasing distance. Assuming that the diminution was uniform, Ratliff and Hartline (1959) predicted the patterns of optic nerve activity generated by various patterns of illumination on the receptor mosaic and verified such predictions experimentally. A more quantitative study of the neural interactions in the *Limulus* eye requires a precise knowledge of the lateral spread of inhibition across the receptor mosaic; that is, an exact law relating the strength of inhibition exerted by one ommatidium

on another to the retinal distance between them. It is the purpose of this paper to present experimental results establishing such a law.

METHOD

Preparation In the experiments to be reported, the methods for excising the *Limulus* lateral eye and for recording impulses from its optic nerve fibers follow those developed by Hartline and his colleagues (Hartline et al., 1956; Hartline and Ratliff, 1957). In each experiment, the lateral eye together with a short length of optic nerve (1 cm) was removed from an adult *Limulus* and mounted in a moist chamber. Small strands separated from the optic nerve were placed on recording electrodes and tested until a strand was found that represented a group of 15–20 ommatidia located near the center of the eye. These ommatidia constituted the "mapping field"; that is, the group of receptors used to map the spread of inhibition from a nearby source. Ommatidia located in the periphery of the eye were avoided because their optical axes diverge 30–40° from the normal to the corneal surface (Waterman, 1954) making optical isolation of single units difficult. A nerve fiber from an ommatidium lying near the mapping field was dissected from the remaining strands and placed on a second pair of electrodes. This ommatidium and its three nearest neighbors made up the "source" of the inhibitory effects that were mapped. The response of only one of the four ommatidia in the cluster was recorded on the assumption that all four units responded, more or less, alike. This assumption seems reasonable since each ommatidium in the cluster received the same light intensity and since, in general, it was found that equal light intensities evoked approximately equal firing rates from a number of ommatidia in a given eye.

Optical Stimulation A system utilizing fiber optics provided a convenient method for precisely illuminating the single ommatidia in the mapping field and the small cluster of ommatidia constituting the inhibitory source. A thin glass fiber (76 μ × 90 cm; American Optical Co., Southbridge, Mass.) brought into contact with the cornea and positioned directly in front of a single ommatidium (about 200 μ in diameter) could "pipe" light into that unit without illuminating nearby receptors. The following steps were taken, however, to ensure the complete optical isolation of the unit. First, about one-half of the cornea was shaved off to remove surface imperfections. This operation also decreased the optical path length between the tip of the fiber and the receptor layer and thus reduced the area illuminated by the divergent light cone (68°) emerging from the fiber. Most of the corneal lens structure remained intact after shaving and assisted in the optical isolation by partially refracting the divergent cone of light into the ommatidium. The size of the cone emerging from the fiber depends on the refractive index of the external medium (Kapany, 1967). It was possible, therefore, to decrease the cone from 68° to 44° by applying mineral oil between the tip of the fiber and the corneal surface. The final step was to align precisely the optical axis of the fiber with that of the ommatidium.

Even though these simple operations virtually guaranteed the complete isolation of single units, the quality of isolation was monitored throughout every experiment. This was done by recording continuously the activities of all units in the mapping

field, thereby enabling each unit to monitor the quality of isolation of neighboring units and vice versa. Poor optical isolation of the unit being tested was signaled by the appearance on the recording apparatus of nerve impulses from neighboring units. This technique, of course, could detect only the scattered light that was intense enough to evoke a discharge from the neighboring units, leaving undetected the very low intensity scattered light that was subthreshold for stimulation. Such subthreshold effects could conceivably have a strong influence on the measurements reported in this paper and, therefore, will be dealt with in detail in the Discussion.

The small clusters of ommatidia were illuminated through a bundle of tightly packed glass fibers (Type LGM-1, American Optical Co.). The light source for the single glass fiber and for the fiber bundle operated in the following manner: a large field lens focused the tungsten filament of a DC regulated lamp (Sylvania DCL projection bulb) onto the field stop of a × 45 microscope objective that in turn focused a reduced image of the field lens onto the tip of the fiber instrument. The light beam was interrupted by an electromagnetic shutter (Hartline and McDonald, 1948), neutral density filters (Kodak Wratten filters), and a variable density wedge (Kodak). A spectral analysis (Model SR Spectroradiometer, ISCO, Lincoln, Nebr.) of the light transmitted through the single glass fiber under maximum illumination by the tungsten light source indicated that the total power output of the fiber from 400–650 mμ was 2.4×10^{14} quanta sec^{-1}. Normally this flux was attenuated by 10^{-4} or more.

Data Collection and Processing In each of the experiments reported here the raw data consist of many trains of nerve impulses recorded from one or more optic nerve fibers. Methods for collecting and processing these data have been developed by H. K. Hartline and associates. In brief, a computer (CDC, 160A), a programmed timer (Milkman and Schoenfeld, 1966), and associated equipment (Schoenfeld, 1964) are integrated to control and monitor an experiment, and to collect, preserve, and process the data. For a detailed description of these methods, see Lange (1965) and Lange, Hartline, and Ratliff (1966).

Measuring the Inhibitory Coefficient The results of initial attempts to map an ommatidial inhibitory field indicated that the strength of inhibition exerted by a single unit was too weak for its field to be measured with precision, whereas the inhibition exerted by a small cluster of four ommatidia seemed adequate. Consequently, the technique employed for mapping an inhibitory field was to illuminate a cluster of four ommatidia and measure its inhibitory influence on a number of nearby ommatidia.

As indicated above, the response of only one of the four receptors within the cluster was recorded on the assumption that all four units responded alike. It was further assumed that the cluster was small enough to approximate a point source of inhibition while exerting, of course, four times the inhibitory effect of a single unit. Under these conditions the strength of the inhibitory effect of the cluster on a nearby unit is linearly related to the response level of the former (Hartline and Ratliff, 1957) and can be given as:

$$e_i - r_i = K_{ic}(r_c - r_{ic}^{\circ}) \qquad (1)$$

where $e_i - r_i$ is the difference between the uninhibited and inhibited response levels of the i^{th} unit in the mapping field. The term $r_c - r_{ic}^{\circ}$ represents the amount by which the response of the cluster (r_c) exceeds the threshold (r_{ic}°) of its inhibitory effect on the i^{th} unit, and following Hartline and Ratliff's terminology K_{ic} is the inhibitory coefficient for the cluster affecting the i^{th} unit. In this case, the inhibitory coefficient measures the strength of inhibition exerted by the cluster on the i^{th} unit. The inhibitory field was mapped by measuring the coefficients for a number of units surrounding the cluster. These measurements were made under steady-state conditions following the method developed by Hartline and Ratliff (1957). One important restriction worth mentioning was that the uninhibited firing rates (e_i) of the units tested in the

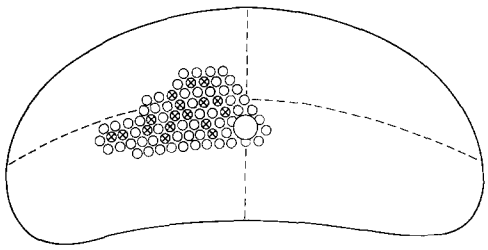

FIGURE 1. A scale drawing of the lateral eye illustrating the arrangement of ommatidia in the mapping field for a particular experiment. The solid line denotes the perimeter of the eye (15 mm × 7 mm); the dorsal direction is down and the anterior direction is to the left. The dashed lines (used as coordinates) divide the eye into equal sections; the anteroposterior line roughly follows the curvature of the cornea. Each of the small circles represents an ommatidial facet. The circles containing x's represent the facets of ommatidia in the mapping field; that is the ommatidia whose nerve fibers are placed on recording electrodes behind the eye. The large circle below the intersection of the dashed lines indicates the location of the fiber optics bundle.

mapping field were adjusted to 25 impulses/sec to maximize the measured coefficients. Further information on this restriction and on other details of the measuring techniques is given elsewhere (Barlow, 1967).

RESULTS

The scale drawing of the lateral eye in Fig. 1 illustrates for a particular experiment the location of the source of inhibition and of the nearby ommatidia that constitute the mapping field (refer to Method section). The relative magnitudes of the inhibitory coefficients for the receptors in the mapping field are shown in Fig. 2 with a three-dimensional model. The coefficients have a finite low value near the source of inhibition, increase to a maximum at some distance from the source, and then decrease monotonically to zero far from the source. These results were obtained from ommatidia located in the anterior direction from the source of inhibition. Measurements from ommatidia located in other directions relative to the source (Fig. 3) indicate that the inhibitory field is not radially symmetrical, but is symmetrical about the

anteroposterior and dorsoventral axes. These results support the earlier measurements by Hartline et al. (1956) who reported that "inhibition diminished with increasing distance, and the diminution was more rapid in the dorsoventral direction than in the anteroposterior." They failed to detect the initial increase of inhibition with distance because their measurements were made at or beyond the inhibitory maxima in each direction.

Assuming that the results given in Fig. 3 are indicative of an elliptically shaped field, a contour map was constructed (Fig. 4) by interpolation of the data. The map encompasses over 30% of the retina or about 300 ommatidia; however, less than one-third of this number receives the bulk (75%) of the inhibitory effects exerted by the cluster. Assuming that each of the four units within the cluster behaves in a similar fashion, an estimate of the strength of inhibition exerted by a single unit was obtained by dividing the observed inhibitory coefficients by four. From the data plotted in Fig. 3, the average value of the maximum inhibitory coefficient for a single unit was 0.06 $\pm$ 0.02 which agrees fairly well with the value of 0.1 published by Hartline and Ratliff. Note that the data illustrated in Fig. 3 have been pooled from experiments on eight lateral eyes from as many horseshoe crabs. In addition, the location on the retina of the cluster and of the mapping field varied from one eye to the next which, considering the small spread in the data in Fig. 3, indicates that the configuration of the field is similar for a large part of the eye.

DISCUSSION

The initial purpose of this investigation was to establish for the *Limulus* eye a law relating the strength of the inhibitory effects exerted between two ommatidia to the retinal distance separating them. However, this could not be done directly because of the difficulties encountered in measuring with accuracy the weak effects exerted between single units (see Method section). As a result, the investigation was carried out using as the source of inhibition a small cluster of four ommatidia.

The Inhibitory Field of a Single Unit

The inhibitory field of the cluster was determined with the hope that its properties would reflect more or less those of the inhibitory field of a single unit. However, with the fragmentary information presently available on the latter, very little can be said about the similarities or dissimilarities between the two fields with one exception: the inhibitory field of the single unit may be less uniform than that of the cluster. This statement is based on the observation by Ratliff and Hartline (1959) that a substantial amount of irregularity exists in the inhibitory action among single units; that is, the strength of inhibition exerted on an ommatidium by one of its near neighbors often differs from that exerted by another neighbor at the same distance from it.

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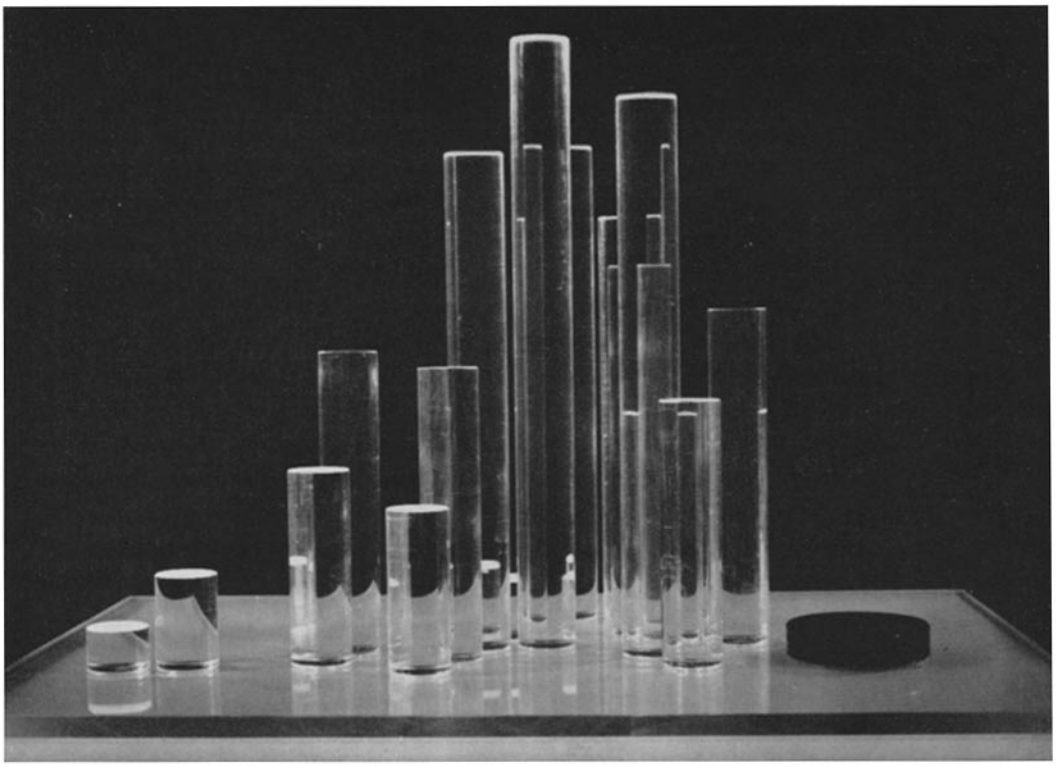

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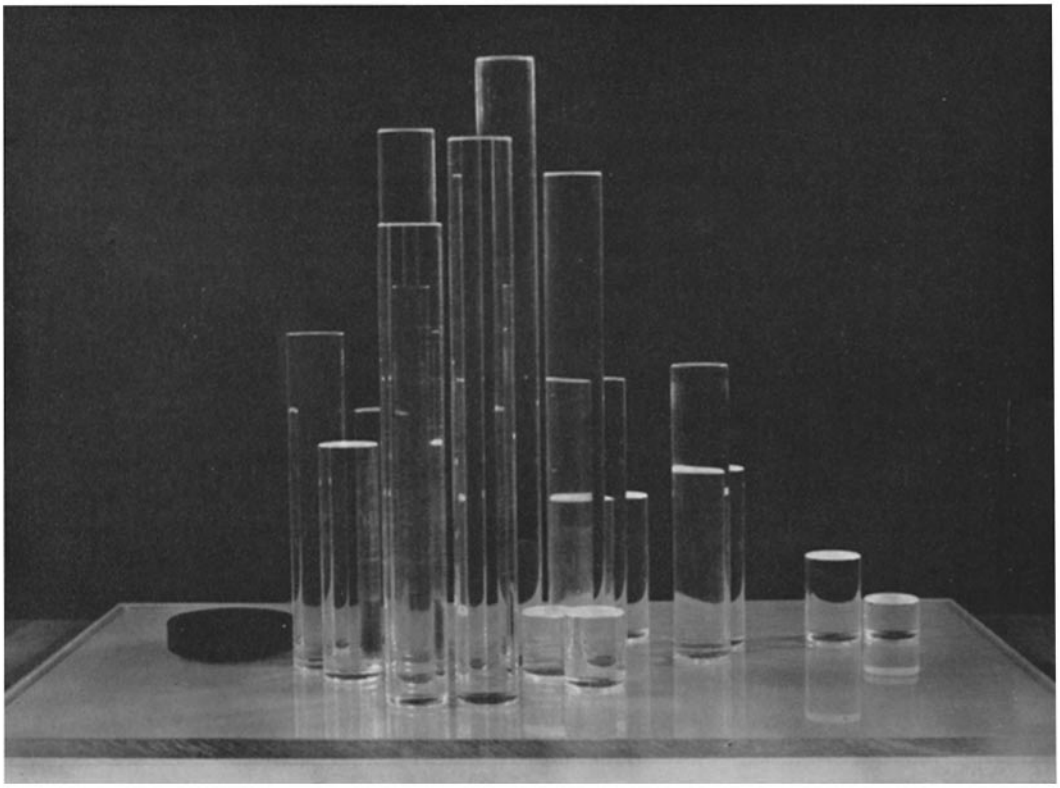

These irregular effects, however, are likely to diminish when an ommatidium is inhibited by two or more units. For example, when two adjacent units inhibit a third, a weak effect from one may be offset by a strong effect from the

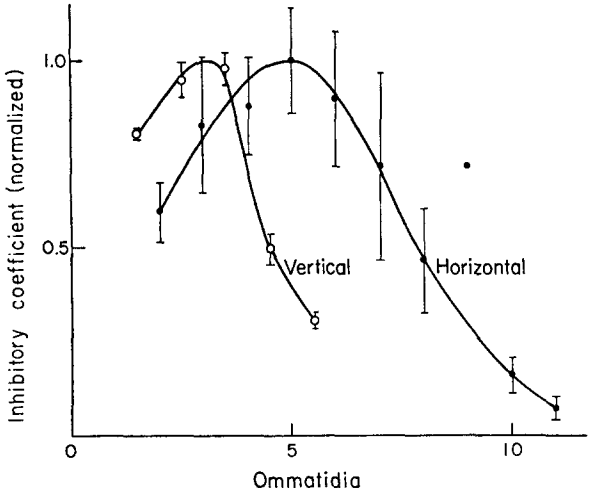

FIGURE 3. The dependence of the magnitude of the inhibitory effect on the separation of ommatidia in the retinal mosaic. The magnitude of the effect (measured by the "normalized" inhibitory coefficient) is plotted on the ordinate as the function of the distance from the source of inhibition in ommatidial diameters on the abscissa. The coefficients measured in the dorsal and ventral directions from the source of inhibition are nearly identical and are plotted together on the "vertical" curve; the same is true for the anteroposterior or "horizontal" direction. Each point on the vertical curve is the average of four to five experiments with one exception: the point above the word horizontal represents the only measurement made at the ninth position in the anteroposterior direction. The standard deviation of the data is indicated by the vertical bars. The data are normalized by assigning the maximum inhibitory coefficient in each experiment a value of one and adjusting the other coefficients proportionately. For theoretical considerations the two curves can be approximated by Gaussian functions: the vertical curve with a function having a peak value of 0.06 which decreases by 1.25 S.D. units at two ommatidial diameters on either side of the peak; the horizontal curve with a function having the same peak value of 0.06 which decreases by 1.5 S.D. units at four ommatidial diameters.

other; the more units involved, the greater the likelihood of irregular effects from one unit offsetting those from another. Therefore, it is suggested that the uniform appearance of the observed inhibitory field is the result of summing

FIGURE 2. A three-dimensional Lucite model illustrating the magnitude of the inhibitory effect exerted by a cluster of four ommatidia at various distances from the cluster. Figs. 2 A and B are different views of the same model. The black disc represents the location on the eye of the fiber optic bundle, 500 μ in diameter, illuminating the cluster. The transparent Lucite rods correspond to the ommatidia in the mapping field and are located in the model according to the arrangement in Fig. 1. The height of each rod is proportional to the inhibitory coefficient (K_{ic}). Fig. 2 A is a ventral view of the model with the anterior direction to the left; Fig. 2 B is a dorsal view.

together four somewhat more irregular fields, one from each unit in the cluster.

Interpretation of the Inhibitory Field

The first measurements of the spread of inhibition in the *Limulus* eye (Ratliff and Hartline, 1959) demonstrated that the strength of inhibition exerted by one unit on another diminishes uniformly as the distance between the units increases. These results were confirmed indirectly by an analytical study of the eye's response to various patterns of illumination (Kirschfeld and Reichardt, 1964). However, the present findings show that the decrease of inhibition with distance occurs only in the outlying region of the inhibitory field; that is, for interommatidial distances greater than 1 mm (four or five receptor diameters). In the central region (interommatidial distances less than 1 mm) the effect reverses: inhibition increases with distance. This is indeed the most striking feature of the inhibitory field. It was not detected by Ratliff and Hartline because their measurements were made on ommatidia separated by more than 1 mm. Nor was it detected by Kirschfeld and Reichardt because the variability of their individual measurements did not permit the observation of the weak, higher order effects which would reveal the double Gaussian field (Reichardt, personal communication). Its origin is not known, but several possibilities will now be considered.

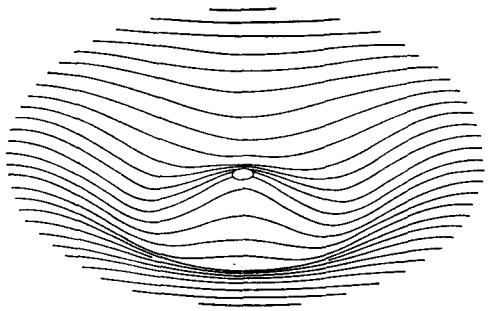

FIGURE 4. A three-dimensional map of the inhibitory field in parallel perspective. The map was constructed using the methods of cartography outlined in Jenks and Brown (1966). The major axis (anteroposterior) of the inhibitory field lies horizontally. The open circle corresponds to the area occupied by a single ommatidium. The curvature of lines immediately surrounding the open circle is based on data extrapolated from Fig. 3.

It is reasonable to suppose from what is known about the anatomy and physiology of the *Limulus* eye (Hartline, Ratliff, and Miller, 1961) that the configuration of the inhibitory field is determined by the organization of the lateral plexus, an extensive network of fine nerve fibers that mediates inhibition between ommatidia. The results of the present experiments could be ex-

plained by a particular arrangement of the plexus in which the number of connections between ommatidia increases with distance, reaches a maximum, and then diminishes gradually to zero. If this interpretation were correct, then the curves in Fig. 3 would represent the distribution of inhibitory contacts between a given receptor and its neighboring units. Other arrangements of the plexus could produce the same results. Evidence supporting this or similar interpretations would have to come from anatomical studies of the inhibitory pathways in the lateral plexus; however, such studies have not yet been possible with the histological techniques presently available.

It is important to note that the configuration of the observed field can be represented by combining the effects of inhibition and excitation. For example, consider the scheme in which both effects are maximal at the center of the field, the inhibition always outweighing the excitation, and both diminish with increasing distance from the center, the rate of diminution being more rapid for the excitatory effect. The resulting field would be similar in every respect to the contour map in Fig. 4; that is, have a "triphasic" shape with no measurable excitatory component. To test this scheme, an attempt was made to find an as yet undetected excitatory effect. Two possibilities were considered: scattered light and local neural excitation.

SCATTERED LIGHT The magnitude of the inhibitory effects exerted on ommatidia near the center of the field may have been diminished by inadvertently exciting these units with light scattered from the fiber optic bundle located over the cluster of ommatidia that constitute the source of inhibition. If this indeed were the case, then the excitatory effect from such scattered light would be exerted in the same region where the observed inhibitory effects are depressed. However, with the stimulating and recording methods used in these experiments, the intensity of scattered light from the fiber bundle was known to be too weak to initiate responses from receptors outside the desired area of illumination. Nevertheless, it is possible that "subthreshold" scattered light from the bundle could have increased the response of a neighboring unit by acting in concert with light shone upon that unit when its inhibitory coefficient was determined. This possibility was tested by introducing the equivalent of scattered light and measuring its effect on the firing rate of an ommatidium.

The results from two such tests are given in Fig. 5 which plots the increase in the firing rate in response to a small increment (ΔI) in the light intensity, (I), on the ordinate vs. the firing rate in response to ΔI alone on the abscissa. In each test, ΔI mimics the effect of scattered light, and I represents the intensity used to illuminate ommatidia in the mapping field. In order to attribute the central depression in the inhibitory field to excitation from scattered light, ΔI added to I must increase the response by at least 1.5–2 im-

pulses per second when the response to ΔI alone is zero. Indeed, this is not the case. ΔI added to I does not increase the response to I when the response to I alone is zero (as indicated by the points at the origin). Therefore, scattered light which is too weak to initiate impulses on its own can have no measurable excitatory effect in a mapping experiment. In fact, to produce the effects observed in these experiments requires scattered light that would yield some 5–10 impulses per second, acting alone.

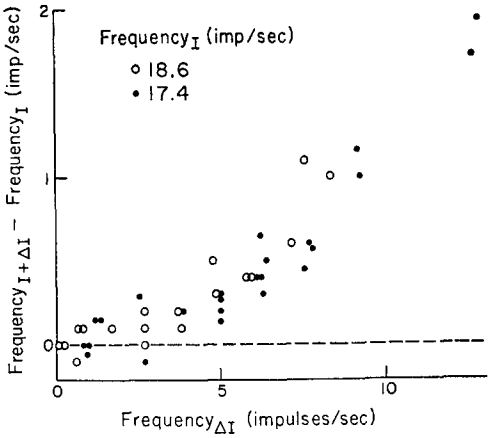

FIGURE 5. The steady-state response of an ommatidium to small increments in the incident light intensity. The data from two separate experiments on different ommatidia are plotted together. The steady "background" intensity, I, evoked a discharge of 18.6 impulses/sec from one of the ommatidia (open circles) and 17.4 impulses/sec from the other (filled circles). The increase in the response of either ommatidium to a small increment, ΔI, of the background intensity, I, is plotted on the ordinate as a function of the response to ΔI alone on the abscissa. The transient effects resulting from the increments in light intensity are neglected—only steady-state responses are considered.

LOCAL NEURAL EXCITATION The membrane potential of an ommatidial eccentric cell becomes hyperpolarized when the activity of the ommatidium is inhibited either by the illumination of nearby ommatidia (Hartline et al., 1961) or by the antidromic stimulation of the optic nerve fibers (Tomita, Kikuchi, and Tanaka, 1960). When the latter method is used, the observed hyperpolarizations are often preceded by small depolarizations (Tomita et al., 1960; Purple, 1964) indicating that excitation as well as inhibition can be transmitted laterally in the eye. Such excitatory depolarizations have not been detected when inhibition is caused by the illumination of nearby ommatidia as is done in the present experiments. Nonetheless, if excitatory effects are transmitted between ommatidia under the conditions of the present experiments, then it should be possible to separate them from the inhibitory effects by selectively abolishing the latter with ethanol (MacNichol and Benolken, 1956).

Several attempts to do this were made by studying the effects of small amounts of a 4% solution of ethanol in seawater, injected through a hole (300 μ) in the cornea, on the interaction between one ommatidium and a small cluster of four. In each attempt, the injection of 1 μl of the ethanol solution abolished within 1 min the inhibitory effects exerted by the cluster on the single unit, the effects returning to full strength within a few minutes following the injection of several microliters of seawater. It was found that *no* excitatory interactions could be detected under any conditions. Presumably the mechanism of action of ethanol in the *Limulus* eye is to selectively block the synapses that mediate inhibition as suggested by the observations of Bernhard and Skoglund (1941) on the vertebrate retinal ganglion cell. However, ethanol in sufficient quantities can depress the general excitability of nerve cells (Moore, Ulbricht, and Takata, 1964) and thereby, could mask the possible excitatory effects in the *Limulus* eye. This seems unlikely since it was found that excessive amounts of ethanol, 5–10 times the amount necessary to abolish inhibition, were required to depress measurably the response of an ommatidium.

Apparently, the lateral excitatory effects found by Tomita et al. and Purple are too weak to have a measurable effect on the response of an ommatidium when inhibition is abolished with ethanol, and presumably the same holds true in the absence of ethanol. Therefore, the complex configuration of the inhibitory field is probably not caused by competing excitatory and inhibitory effects, but rather is an expression of the particular mode of interconnections between ommatidia. However, any discussion at this time of the organization of the plexus of neural interconnections can only be speculative.

Inhibitory Thresholds

The term, r_{ic}°, in equation (1) represents the response threshold that the cluster must exceed before it can inhibit the i^{th} receptor unit. Experiments by Ratliff and Hartline (1959) indicated that the thresholds may be inversely related to the inhibitory coefficients; that is, the greater the separation between units, the higher the thresholds. The results of the present mapping experiments were expected to support these observations. However, the data are not consistent. In several experiments the thresholds and coefficients are inversely related as in Ratliff and Hartline's experiments; in other experiments they are directly related; and in still other experiments there seems to be no relationship at all. No firm conclusions can be drawn from these experiments concerning the relationship between the thresholds and coefficients.

Inhibitory Fields: Limulus vs. Vertebrate

There are no reported studies on inhibitory fields in retinas comparable in organization to that of the *Limulus* eye; however, an extensive amount of

work has been done on the vertebrate retina, dating back to Hartline's studies (1938, 1940) on the frog, alligator, and other cold-blooded vertebrates. In the vertebrate retina, the counterpart of the *Limulus* ommatidium or more precisely of the eccentric cell of the ommatidium is the ganglion cell. Both cells perform similar functions; that is, both transmit visual information to the brain via their associated optic nerve fibers. In addition, the response of both cells is determined to a greater or lesser extent by the activities of neurons in neighboring retinal areas. The retinal area from which a ganglion cell response can be elicited was originally defined by Hartline (1938, 1940) as the receptive field of the cell. This definition has since been extended by Kuffler (1953) to include all areas within which stimulation can excite or inhibit the ganglion cell response. In *Limulus* the inhibitory field of an ommatidium is defined as the location on the receptor mosaic of ommatidia that receive inhibition from that unit.

It is apparent that the interactions in the two retinas differ in at least one important respect: in the vertebrate retina the interactions are both excitatory and inhibitory, whereas in the *Limulus* retina the interactions are predominantly inhibitory. Comparisons between the two retinas should therefore be limited to the common property of inhibition; that is, the inhibitory field in *Limulus* should be compared only to the inhibitory component of the vertebrate receptive field.

Separation of the vertebrate receptive field into its component parts is difficult because the excitatory and inhibitory influences usually respond to the same stimuli. This is not true in the eye of the goldfish where the opposing influences may be chromatically separated (Wagner, MacNichol, and Wolbarsht, 1963). These receptive fields have overlapping excitatory and inhibitory components with maximal light sensitivities in the center of the field that diminish at different rates toward the periphery so that one influence predominates in the center, the other in the surround. The surround influence of the inhibitory type has several features in common with the *Limulus* inhibitory field. In each case the inhibitory effects are exerted throughout the field, and more importantly the effects are graded with distance from the field center. This statement must be qualified by adding that the inhibitory effect in the *Limulus* eye first reaches a maximum before tapering off in the periphery. The uniform diminution of the surround component in the peripheral regions of the goldfish receptive field is characteristic of most vertebrates and is the point of greatest similarity between the *Limulus* inhibitory field and the vertebrate receptive fields. The spread of the so-called surround component throughout the entire field is probably not characteristic of all vertebrate receptive fields. For example, in the retina of the ground squirrel, Michael (1968) found three types of receptive fields: one with complete spatial overlap of the excitatory and inhibitory components, another

with partial overlap, and a third with no overlap. Moreover, there is evidence that some vertebrate receptive fields are not arranged into two concentric and antagonistic regions as are those mentioned above but have highly complex spatial distributions (Spinelli, 1966). These fields most likely perform highly specialized functions such as line and edge detection. They seem to bear little resemblance to the *Limulus* inhibitory field.

Most vertebrate receptive fields that have been investigated are divided into concentric regions having antagonistic functions that do not respond to the same stimuli as in the goldfish and ground squirrel. Cross-sections of these fields are characteristically triphasic in shape; that is, have a central component of one influence (either excitatory or inhibitory) flanked by maxima of the opposite influence. According to some analyses, the configuration of these fields is the result of opposed fields of excitation and inhibition. For example, Rodieck and Stone (1965) found that some receptive fields in the cat retina could be represented by the sum of two Gaussian functions, a narrow positive one for excitation and a wider negative one for inhibition. With a model incorporating these functions, Rodieck and Stone predicted accurately the response of cat retinal ganglion cells to moving stimuli. The *Limulus* inhibitory field is also triphasic in shape (Fig. 4). The possibility that the shape of this field represents the combination of two opposed fields was considered (see section on the Interpretation of the Inhibitory Field) and rejected because no excitatory influences could be detected. Nonetheless, in both fields, the maximum inhibitory effects are displaced from the center of the field. These eccentric maxima may play a significant role in "tuning" the visual system to particular frequencies of periodic spatial stimuli (Ratliff, Knight, and Graham, 1969).

I wish to acknowledge the advice and criticism of Drs. H. K. Hartline and Floyd Ratliff. The research reported in this paper was performed in their laboratory. I would also like to thank Drs. David Lange, Fred Dodge, and Mr. Bruce Knight for their many helpful discussions.

This paper is based on a dissertation submitted to the faculty of The Rockefeller University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

The preparation of this manuscript was supported by National Institutes of Health grant number NB-03950-07.

Received for publication 17 February 1969.

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