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Receptor Mechanisms and the Integration of Sensory Information in the Eye

H. K. HARTLINE

The Rockefeller Institute, New York 21, New York

THE processing of sensory information begins in the sense organs themselves. It is in them that the first steps take place in the transformation of external influences into the patterns of nervous action that regulate the activity of an animal in its complex environment. The fundamental nature of the receptors and the design of the accessory structures in which the receptors are deployed determine how external information flows into the organism. Thus, sense organ and receptor mechanisms determine the character of the neural activity that is passed on to higher neural centers. In addition, the first steps in neural integration take place within the sense organs, for in many of them the receptors interact with one another. As a result of both of these actions, patterns of sensory nerve fiber activity transmitted to the higher centers are more than mere replicas of the temporal and spatial patterns of external stimuli. Certain significant features of the stimulus patterns are accentuated at the expense of less important fidelity of representation. This can be clearly illustrated in the analysis of the first steps of the visual process, with which this paper deals.

One of the great contributions of biophysics in the last century was the precise description of the human eye as an optical instrument. The high degree of perfection of our eyes enables us to exploit many of the peculiar advantages of luminous energy as a source of information; their shortcomings set limits to our visual performance. The vertebrate scheme of optical imagery by a lens system is not the only one that is used by animals; compound eyes also have been evolved—made up of small optical units, each having a narrow entrance angle and each pointed in a different direction so that all cover the entire field of view. They too have both advantages and disadvantages, one of the advantages being that short wavelengths can penetrate to their receptors. In either case, retinal receptors arranged in a mosaic receive light in varying amounts from the various parts of the animal's surroundings. The mechanism of the visual receptor units that compose the retinal mosaic determines many of the properties of vision.

The photoreceptor offers certain advantages over many other receptors in the study of sensory mechanisms, for in it the very first step in the transducer mechanism for translating the stimulus into nervous action is beginning to be well understood. This is a consequence of the general principle that electromagnetic radiation, to produce a permanent effect on a material system, must yield some of its energy to the system. Consequently, the action spectrum of the visual apparatus is simply the manifestation of the absorption spectrum, or a portion of it, of the primary photosensitive material in the visual receptors. It is the absorption spectrum of the primary visual pigment that sets the rather indistinct limits to the extent of the visible region within the electromagnetic spectrum and that determines quantitatively the relative effectiveness of different wavelengths of visible light. There is now very good agreement between the measurements of the absorption spectrum of photolabile pigments extracted from the retina and the "action spectrum" of vision for several animal forms, especially for man.[1,2]

The fact that one can identify the photosensitive material of the visual receptor makes it possible to say whereabouts in the receptor cell the first act of the visual process takes place. In the vertebrate eye, the visual pigment "rhodopsin" is known to be concentrated entirely in the outer segments of the retinal rods. This identifies the outer segments as the locus of the initial step in the visual receptor process. Rhodopsin can be extracted from suspensions of the outer segments of retinal rods, and its absorption spectrum, after appropriate correction, agrees well with the distribution of spectral sensitivity of rod vision. It is clearly the primary photosensitive substance of the rods. A number of visual pigments related to rhodopsin are now known. One of them, iodopsin, is the corresponding photosensitive substance of the retinal cones.[3] The biochemistry of the visual pigments constitutes an extensive and elegant chapter of modern biochemistry that cannot be discussed in detail in this paper (cf. Wald[4]).

Rhodopsins are known to be conjugated proteins, the prosthetic group being a carotenoid called retinine. Retinine is an aldehyde, the corresponding alcohol being vitamin A, and is known in a number of isomeric forms. The first act of light apparently is to produce an isomerization of the carotenoid group while it is still attached to the protein.[5] Retinine is then split off the protein molecule by subsequent reactions that are independent of light, and may be converted reversibly into vitamin A.

After photolysis, visual pigments can regenerate. Otherwise, one would have one look at the world and then be forever blind. The kinetics of photolysis and regeneration of visual pigments has been studied extensively, both *in vitro* and recently in the living retinas of experimental animals and human subjects.[6] Many

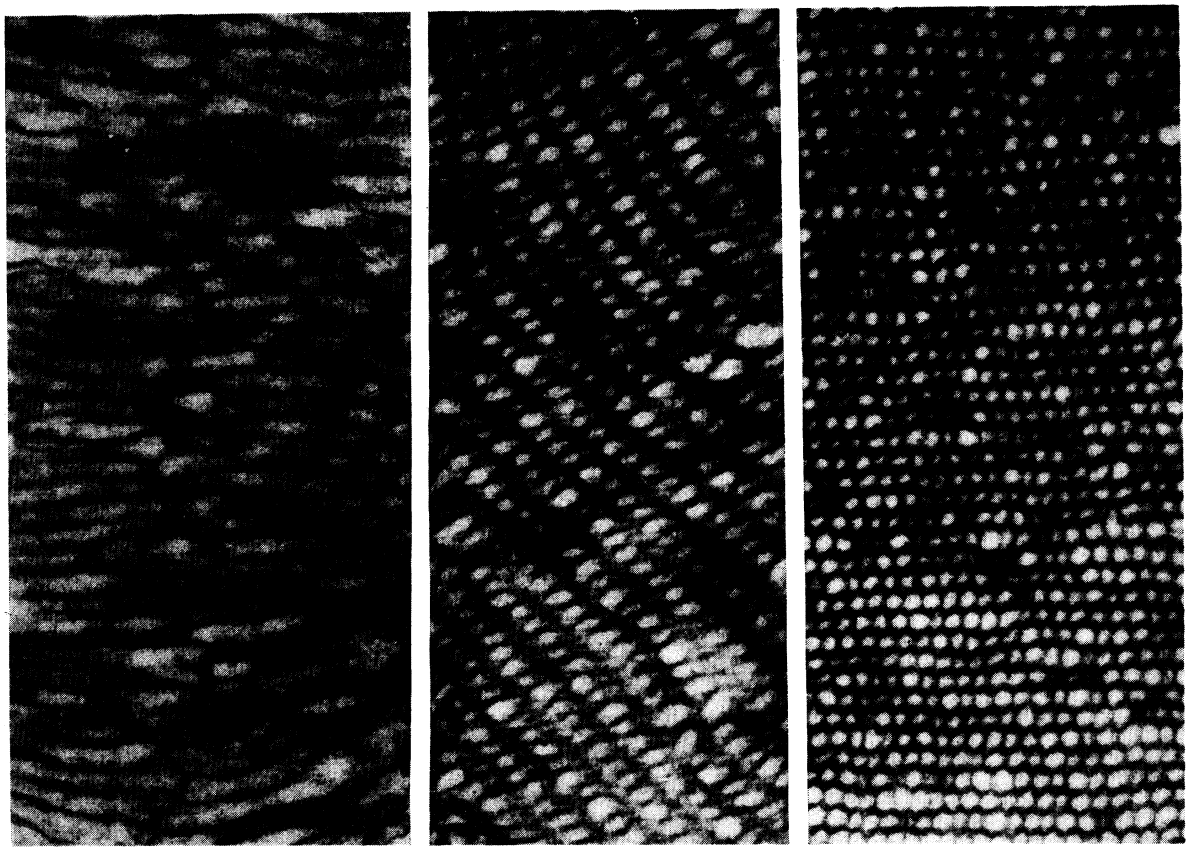

FIG. 1. Electron micrographs of rhabdom of an ommatidium of an arthropod compound eye (*Limulus*), showing honeycomb-like arrangement of osmium-staining membranes. Left: plane of section perpendicular to optical axis of ommatidium. Center: oblique section. Right: section in an axial plane. Height of figure approx 2 μ. Courtesy W. H. Miller.

receptor properties, such as the loss of sensitivity in the light and its recovery during dark adaptation, can be explained qualitatively by these elementary biochemical processes in the visual receptors. Moreover, a simple model of the photochemical system of the receptor was used by Hecht to explain quantitatively many psychophysical measurements of vision.[7] His formulations remain the most comprehensive and successful theoretical treatment of visual-receptor physiology, although his model is oversimplified and the theory needs reworking in light of recent developments in biochemistry and physiology.

The primary photosensitive pigment of the visual receptor is present in a structured system. Electron-microscope studies show a profusion of osmium-staining membranes in visual receptors. Sjöstrand[8] has shown that the outer segments of the receptors of the vertebrate retina have a lamellar structure. The rod outer segment is thus a stack of thin plates crowded with rhodopsin. In the arthropods, instead of a lamellar system, the part of the receptor cell (the rhabdom) that presumably contains the visual pigment is composed of myriads of microvilli densely packed to form a honeycomb-like structure. Figure 1 is an electron micrograph of the rhabdom of an ommatidium of an arthropod compound eye.[9] In the vertebrates, the outer segments of the retinal rods and cones have been shown to be derivatives of cilia.[10,11] In the arthropods, where cilia are extremely rare, there is no evidence of a ciliary derivation. In some mollusks, however, there is a different system of membranes and again the structures are derived from cilia.[12] Exactly how the visual pigment is arranged within any of these membranous structures is not known, though there have been speculations on this point.

Visual receptors have evolved into light detectors that are so sensitive that they work at the limit set by the quantum nature of light. A human observer is able to see a flash of light that contains only about 100 quanta, measured at the cornea of the eye. After correction for losses in transmission through the ocular media and failure of the visual purple to be present in sufficient amount in the retina to absorb all of the quanta that fall on it, this figure comes down to something of the order of 10 quanta.[13] This aspect of visual physiology has been extensively studied and is well reviewed in a recent article by Pirenne.[14] Obviously, it is of great significance to visual performance, especially at low

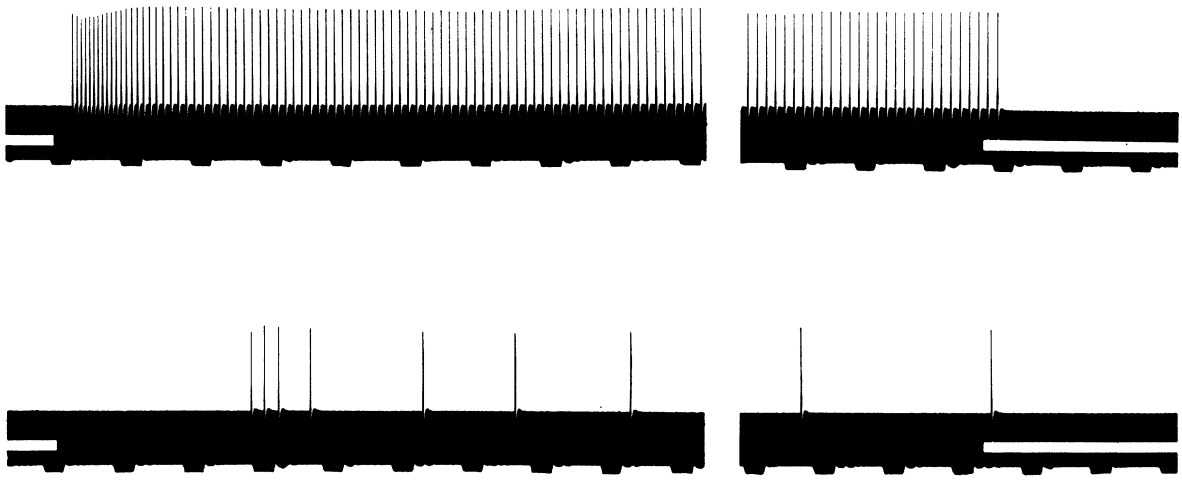

FIG. 2. Oscillograms of the electrical activity in a single optic-nerve fiber (eye of *Limulus*) in response to prolonged steady illumination of the facet of the eye innervated by the fiber.[15] Each spike is the "action potential" associated with the passage of a nerve impulse in the fiber. For the top record, the intensity of stimulating light was 10^4 times that used for the bottom record. Signal of exposure to light blackens out the white line above the time marks. Time marked in $\frac{1}{5}$ sec.

illuminations. In the short "action time" of the retina, so few quanta are needed that the retinal image, though visible, is too "grainy" to be seen with high resolution. Also, at threshold, seeing is uncertain. Indeed, the statistical uncertainty at threshold can be explained almost entirely by the fact that a very few quanta suffice to excite a response. Nevertheless, the visual threshold is sharp enough so that it is quite certain that a human observer cannot see just one quantum, although exactly how many are needed is still a matter of controversy. The small amount of light that is just visible can be seen if it is spread over a retinal area containing about five hundred rods. This must mean that near threshold there is almost no chance of any one rod receiving more than one quantum, and that the cooperative activity of several rods is necessary to reach the threshold of vision. Thus, a single quantum of light absorbed within the stack of plates comprising the outer segment of a rod is sufficient to excite that rod, causing it to transmit some kind of nervous influence that can sum with similar influences from several other rods to reach the threshold for a behavioral response. In this retinal summation, one has an example of the simplest kind of neural integrative action, exerted at the very threshold of vision.

The end result of receptor excitation is the generation of nervous influences in its attached nerve fiber. It has not yet been possible to record the neural activity of the receptors (rods and cones) of the vertebrate retina, but some invertebrate eyes afford an opportunity to record optic activity that appears to be very close to the action of the primary receptors. The eye of the common horseshoe crab, *Limulus*, is particularly favorable for the study of the action of single receptor units. This eye is a coarsely facetted compound eye. Individual receptor units corresponding to each facet (ommatidia) can be separately illuminated, and the electrical activity of the optic nerve fiber from such a unit can be recorded.[15]

The neural activity recorded from one of the receptor units of the eye of *Limulus* consists of trains of uniform nerve impulses similar in all respects to the sensory discharges observed in nerve fibers in all of the higher animal forms (Fig. 2). As in all receptors, the higher the intensity of the stimulus, the higher the frequency of the impulses with which the receptor responds. In the visual receptor, it is noteworthy that frequency changes over a relatively small range for a large range of light intensity: the dynamic range of a single receptor is five or six orders of magnitude. Roughly, the relation between frequency of discharge and intensity of light is a logarithmic one (Fechner's Law). Thus, the transducer mechanism of the visual receptor covers a large range and is adapted to signal the ratios of stimulus values. In our own visual experience, values of light and shade stay more or less fixed, no matter what the ambient level of illumination, over a large range. In such situations, stimulus ratios stay constant and the visual receptors yield approximately a fixed difference in the frequency for a given ratio of stimulus values, even though the absolute differences may vary widely.

Another important receptor property is illustrated in Fig. 2. The discharge of nerve impulses begins at a high frequency when the light is turned on, but the frequency of the discharge subsides in a fraction of a second to a considerably lower level, which is then maintained with only slight diminution as long as light continues to shine on the receptor. This sensory adaptation is manifested by all other receptors, some to a far greater extent than others. As a result of sensory adaptation, receptors provide a somewhat distorted report of the stimulus events, such as to accentuate any sudden change. Sensory trans-

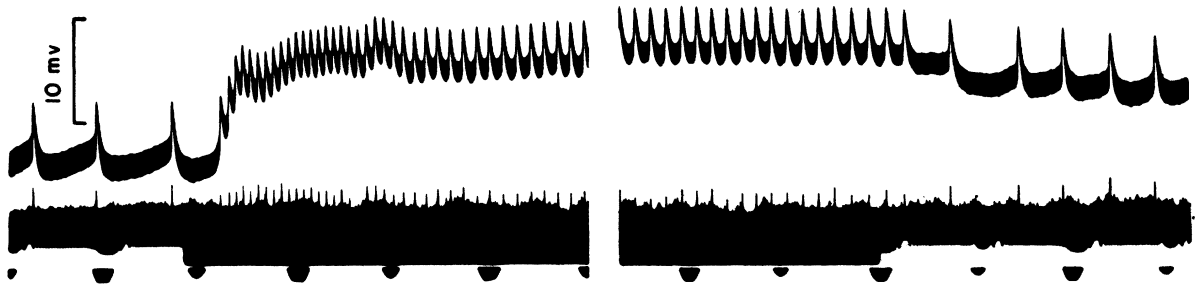

FIG. 3. Electrical responses to illumination of a single receptor unit (ommatidium) in the eye of *Limulus*.[15] Recorded (upper trace) by a micropipette electrode (tip diam 1 μ) in the neuron of the ommatidium, and simultaneously (black edge just below upper trace) by a pair of wire electrodes over which was slung the nerve bundle from the ommatidium containing the neuron's axon. At the beginning of the record, the microelectrode base line records the resting level of the electrical polarization of the cell membrane, at a potential about 50 mv negative to the solution bathing the outside of the cell. When the ommatidium was illuminated (black band above the time marks), there was a partial depolarization of the neuron (potential becoming less negative: rise in the base line) accompanied by an increase in the frequency of the spike-like deflections, each one of which was synchronous with the discharge of an impulse in the nerve bundle (small spikes on the black edge). Time marked in $\frac{1}{5}$ sec.

ducers are not concerned so much with a faithful representation of the world as with a useful one, and it is especially useful to the organism to accentuate the *changes* that occur in external conditions. If the illumination on a visual receptor unit is given a small increment, the receptor response consists of a modulation of the discharge of impulses in which there is an exaggeration of frequency changes at the onset and again when the increment is turned off. This permits the receptor to signal small changes, and still possess a large dynamic range. But what may be even more important, the suddenness of the changes enhances their stimulating effectiveness. Thus, the inherent properties of the sensory receptors determine how the patterns of neural activity they generate will represent the stimulus events. This is a first step in the processing of information for use by the organism.

As yet not much is known about the nature of the excitatory processes following the initial photochemical reaction in visual receptors until one comes near the end of the receptor process. In the eye of *Limulus*, it has been possible to learn a little about the actual production of nerve impulses in the axon of the excited neuron in the receptor unit. By the use of a micropipette electrode penetrating the sensory structure of the ommatidium, changes in the electrical polarization of the cell membrane of the neuron in the ommatidium have been recorded.[15–17] These changes are associated with the trains of impulses initiated by this cell when the receptor unit is illuminated (Fig. 3). When light is turned on, the cell membrane becomes somewhat depolarized, and simultaneously there is a speeding up of the discharge of impulses in its axon. Such depolarization is referred to as a "generator potential,"[18] in the belief that the nerve impulses are generated by local electric currents flowing as a result of the difference in potential between the axon and the depolarized cell body (or more probably, in the present case, the depolarized dendritic process of the cell which penetrates the rhabdom of the ommatidium). The degree of depolarization depends on the intensity of the stimulating light and in turn determines the frequency of the relaxation oscillations of the membrane of the initial segment of axon in the region where it leaves the cell body and from which the propagated impulses take off. The discharge of trains of impulses by depolarized neurons is a familar process in neurophysiology. For the photoreceptor, the question is how the initial photochemical reaction produces the depolarization and the ensuing "generator potential." About this, almost nothing is known.

As discussed in the foregoing, the receptor itself by its inherent properties does a certain amount of processing of the information from the outside world. It is concerned with the report only of certain aspects of the physical stimulus that acts on it, and it is not necessarily a high-fidelity recording device. Built as it is, it selects certain features of the stimulus pattern for accentuation. The next step in the processing of sensory information in the visual system concerns the distribution of light over the entire population of visual receptors. A retina, whether in a vertebrate or an arthropod, is more than a mosaic of independent detecting elements. In the vertebrates, it is well known that the retina is a highly organized nervous center. It is really a part of the brain closely applied to a mosaic of sensory receptors. The first step in the neural analysis of the pattern of the retinal image requires the intercomparison of what happens in the various differently stimulated receptors, and a modification of the pattern of neural activity to accentuate important features of the spatial distribution of light over the receptor mosaic. Evidently, it is profitable to do this close to the point where the information is being picked up. In the vertebrate retina, the early neurons in the visual pathway are spread out in correspondence with their associated receptors, and many of the processes in the first step of neural integration apparaently can be done most effectively in the retina itself. This is not a simple process; patterns of activity observed in the optic-nerve fibers in the verte-

(a) (b)

FIG. 4. The plexus of the compound eye of *Limulus*. (a) Light micrograph of a section cut through the eye in a plane perpendicular to its external surface (cornea removed), showing on its upper border a row of the heavily pigmented ommatidia, from each of which emerges a small bundle of nerve fibers (stained with silver by Samuel's method) that contains, together with small fibers, the axon of ommatidium neuron. Connecting these bundles are festoons of fibers, with clumps of neuropile that appear at this magnification as condensations in the meshes of the plexus. Width of figure = 2.2 mm. Photograph by W. H. Miller [from H. K. Hartline, H. G. Wagner, and F. Ratliff, J. Gen. Physiol. **39**, 651 (1956)]. (b) Electron micrograph of a portion of a clump of neuropile in the plexus, showing a few outlines of the fibers composing the clump, within which are numerous small circular outlines interpreted as synaptic vesicles. Width of figure = 1.2 μ. Photograph by W. H. Miller.[19]

brate retina are very complex, and their analysis is difficult. In simpler visual systems, integrative processes can be more readily analyzed. The eye of *Limulus* again affords a good oportunity for such studies.

The neural structure of the compound eye of *Limulus* is much simpler than that of the vertebrate retina or the eyes of more highly developed arthropods, but it is nevertheless a retina: the units of the receptor mosaic are interconnected by a network of nerve fibers [Fig. 4(a)]. The nerve fibers from the ommatidia branch profusely on their way out of the eye to form the optic nerve. Festoons of these branches connect each receptor unit with its neighbors. There are no nerve-cell bodies in this plexus of interconnections, as in more complex retinas, but there are numerous knots composed of a felt-work of very fine branchlets closely intertwined. The fibers in these clumps of "neuropile" are packed with "vesicles" typically present in synapses [Fig. 4(b)]. Evidently, the clumps of neuropile are synaptic regions, where influences are transmitted from one set of

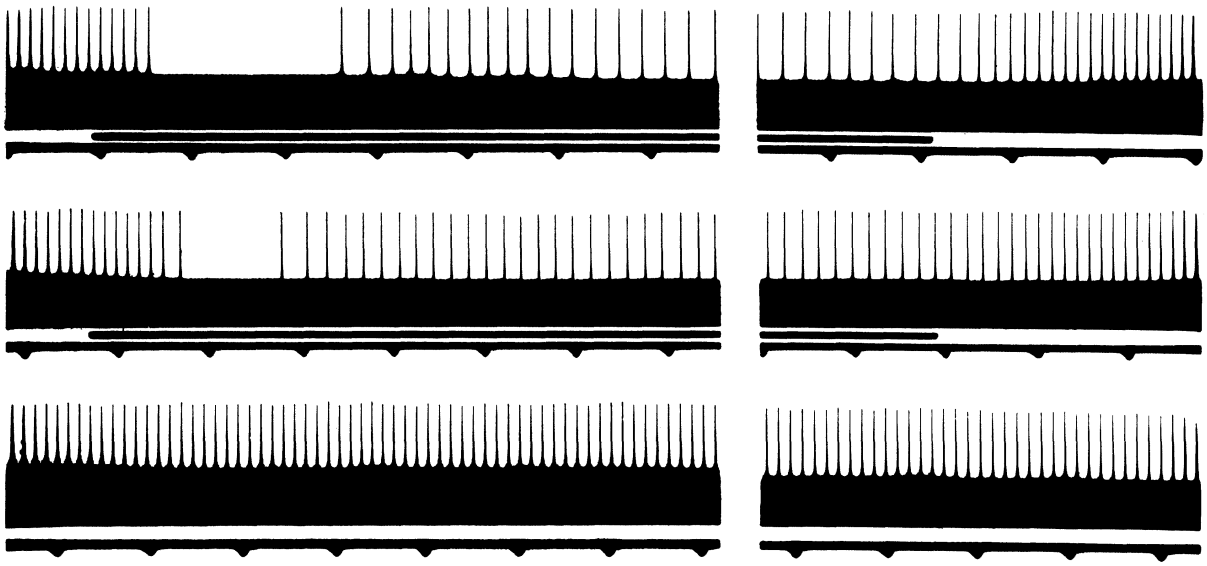

FIG. 5. Oscillograms of nerve action potentials, showing inhibition of the impulses in a single optic-nerve fiber of *Limulus*. The ommatidium of the eye from which the fiber arose was illuminated steadily at a fixed intensity, beginning 3 sec before the start of each of the records; adjacent ommatidium were illuminated during the interval signalled by the blackening out of the white line above the time marks, in the upper two records. In the top record, the intensity of the illumination of adjacent receptors was ten times that used in the middle record. Bottom record is a control (no adjacent illumination). Time in $\frac{1}{5}$ sec. Experimental arrangement as in Fig. 6(a).

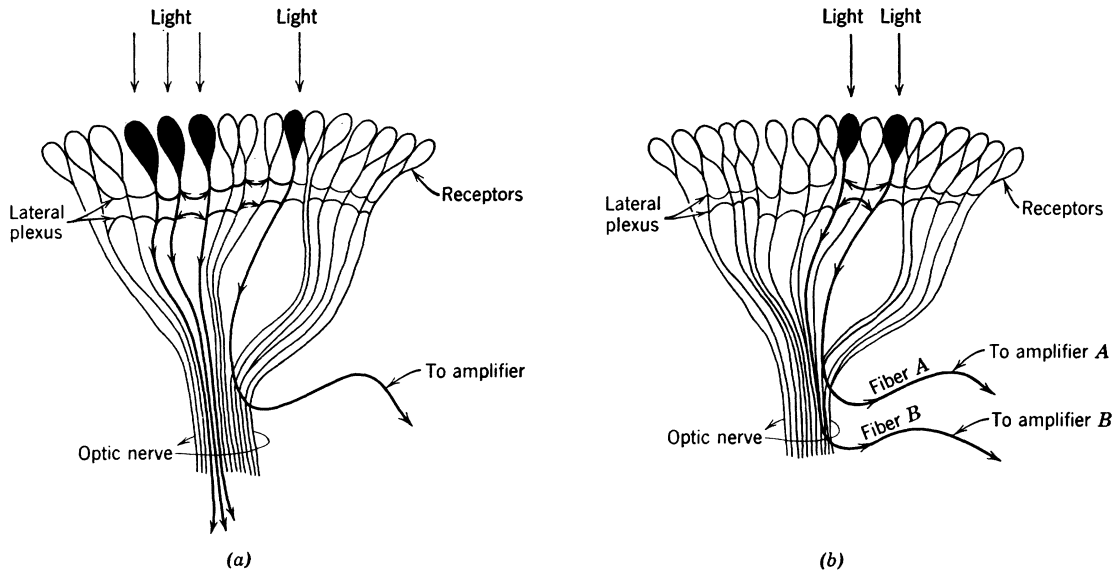

FIG. 6. Schematic diagrams of experimental arrangements used. (a) Experiment of Fig. 5 (inhibition of test ommatidium by illumination of nearby ommatidia). (b) Experiments of Figs. 7 and 8 (mutual inhibition of two ommatidia that were close to one another).

branches to another.[19] Based on this structural organization is a simple functional organization: each ommatidium tends to inhibit the activity of its neighbors. This influence is indeed exerted over the plexus of nerve fibers, for, by cutting the interconnecting branches to an ommatidium, the influence of its neighbors on it can be abolished.

The inhibition that is exerted on an ommatidium by its neighbors is illustrated in Fig. 5. In the experiment from which these records were taken, the discharge of impulses was recorded in a single optic nerve fiber in response to illumination, by a small spot of light, of the facet of the ommatidium from which that fiber arose [Fig. 6(a)]. During steady illumination of that one ommatidium alone, a steady discharge of impulses resulted (bottom record). When, during steady and continuous illumination of this "test" ommatidium, light was caused to shine also on other ommatidia in neighboring regions of the eye (top and middle records of Fig. 5), the frequency at which the test ommatidium discharged impulses was reduced.

Figure 5 also shows that strong illumination of the adjacent region produced a greater depression of frequency than weak illumination. It has also been shown that the magnitude of the inhibition exerted on an ommatidium is greater the larger the number of neighboring ommatidium that are stimulated. Thus, the inhibitory influences from many neighbors can combine to increase the net effect they produce. Also, the inhibition exerted on an ommatidium by its neighbors is greater the closer they are to it. Ommatidia that are separated by a distance exceeding 4 or 5 mm have no effect on one another.

Inhibition in the eye of *Limulus* is exerted mutually by the receptor units.[20] Each ommatidium, being a neighbor of its neighbors, inhibits them as well as being inhibited by them. This is shown in Fig. 7, obtained by recording activity simultaneously in the optic nerve fibers from two independently illuminated ommatidia, close to each other in the eye [Fig. 6(b)]. The frequency of each receptor unit was lower when both were illuminated together than when each was illuminated by itself. When this experiment is performed using various intensities on the two receptors in various combinations, it has been shown that the amount by which the steady frequency of discharge of each receptor unit is lowered depends on the degree of concurrent activity in the other, and is indeed a linear function of the frequency of its discharge (Fig. 8). Thus, the response of one receptor unit is determined by the excitation furnished by the stimulating light shining on it, diminished by the inhibitory influence from the second receptor, which in turn depends on the resultant of the excitation furnished by its own stimulus and the inhibition exerted on it by the first. This mutual interdependence of any two neighboring receptor units may be described by a pair of simultaneous equations, linear in the frequencies of the discharges.

When more than two interacting receptors are illuminated simultaneously, each is subject to the combined inhibitory influences from all of the others. The law that determines how the inhibitory influences from several active receptor units combine in affecting the activity of a neighboring unit has been found by experiment: if the influences on a given unit are measured by the reduction they produce in its frequency of nerve impulse discharge, the combined effect of all of the other units is simply given by the sum of the influences

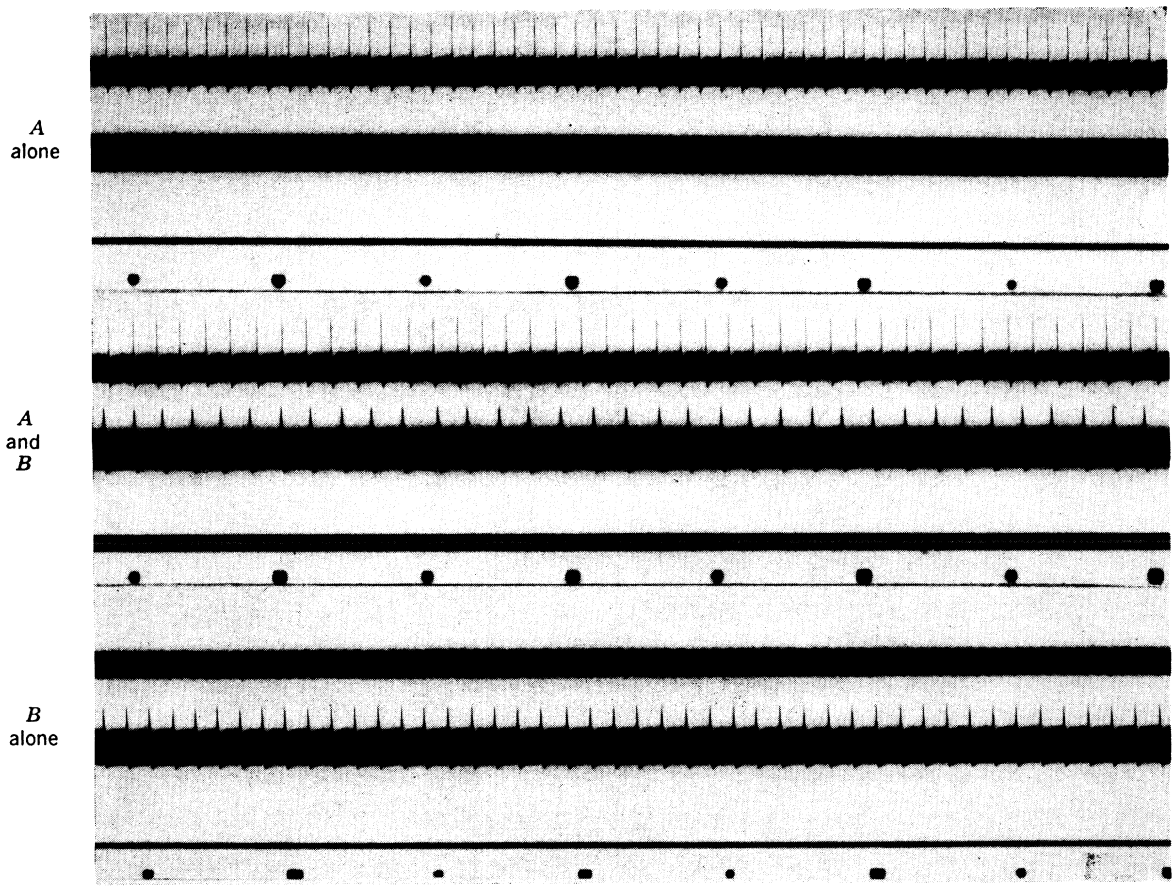

FIG. 7. Mutual inhibition of two ommatidia close to one another in the eye of *Limulus*, steadily illuminated at fixed intensity on each. Experimental arrangement as in Fig. 6(b). Time (black dots) in $\frac{1}{5}$ sec.

exerted by each.[21] The responses of a set of n interacting receptor units, measured by the frequencies of their optic nerve discharges, are therefore expressed by a set of n simultaneous linear equations,

$$r_p = e_p - \sum_{j=1}^{n} K_{pj}(r_j - r_{pj}^0) \quad p = 1, 2 \cdots n.$$

In these equations, r_p stands for the response of the pth unit (measured by its steady frequency of impulse discharge) when it is illuminated steadily together with the other units. Its excitation, e_p, is measured by the response it has when it is illuminated alone. Each constant K_{pj} is the coefficient of the inhibitory action of the jth receptor on the pth (usually less than 0.2) and each constant r_{pj}^0 is the threshold of that action. Terms for which $j=p$ are usually omitted. The equations as written apply only to those units and that range of activity for which r_j is not less than r_{pj}^0. As a rule, the closer the interacting elements are to one another, the larger the K's and the smaller the r^0's. Exceptions are often found, however, and it is not yet possible to state the statistical law governing the effects of distance on the inhibitory interaction.

If N small groups of receptors are considered, each group uniformly illuminated and assumed to consist of receptors with similar properties exerting equal actions, the foregoing set of equations may be reduced to N simultaneous equations with lumped coefficients representing the group interactions. Applied to three interacting receptors or receptor groups, the theory outlined in the foregoing can account quantitatively for a number of effects that have been observed with various experimental configurations of retinal illumination. Thus, if a test receptor is located midway between two groups of receptors that are themselves too far apart to interact, the combined inhibitory action of these two on the test receptor is equal to the sum of the separate actions of each, unless the test receptor itself has an appreciable effect upon them. If the two groups are close together and both are near the test receptor, their combined inhibitory effect will be less than the sum of their separate effects since they inhibit one another mutually when both are active. If a group of receptors is too far from a test receptor to influence it directly, it may nevertheless affect its response by inhibiting a second group located close to the test receptor, thereby releas-

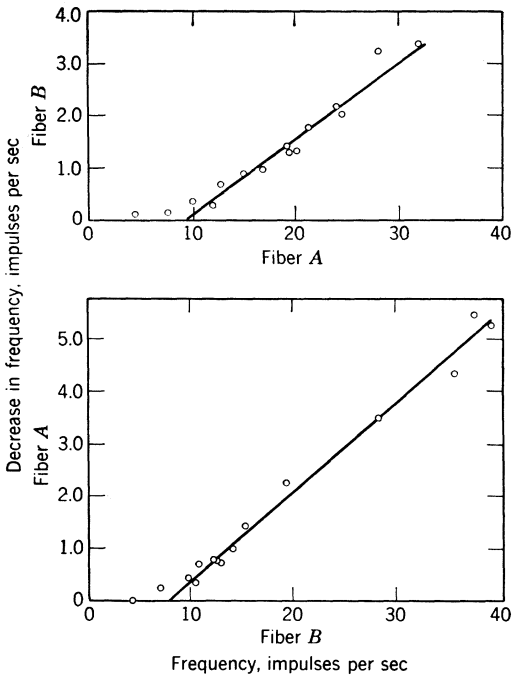

FIG. 8. Mutual inhibition of two ommatidia close to one another in the eye of *Limulus*, illuminated independently at various levels of intensity in various combinations. Amount of inhibition (decrease in frequency) of each ommatidium plotted as a function of concurrent level of response (frequency) of the other. From an experiment similar to that of Fig. 7, experimental arrangement as in Fig. 6(b).

ing the test receptor from the inhibition exerted by the second group. Such "disinhibition" illustrates how indirect effects may be exerted beyond the limits of direct influence and, in principle at least, extend over the entire mosaic of interdependent receptor units.

The inhibitory interaction just described may be considered a simple integrative mechanism that takes place at or close to the level of the receptors themselves. Because of it, patterns of optic nerve fiber activity yield a distorted representation of the patterns of incident illumination. This distortion, however, serves a useful function, for it is clear that inhibitory interaction must enhance contrast: brightly lighted elements in the receptor mosaic inhibit the dimly lighted ones more than the latter inhibit the former. If, as in the eye of *Limulus*, mutual inhibition is greater between close neighbors than distant ones, contrast will be greatest near regions of steep intensity gradients and borders and edges in the retinal image will be "crispened." Phenomena of border contrast are illustrated in our own vision by the light and dark bands bordering a penumbra (Mach bands), and by the fluted appearance of an optical step-wedge or of shadows cast by multiple light sources. Inhibitory interaction is probably one of the mechanisms in our own visual systems that gives rise to these phenomena.[22]

Direct experimental demonstration of the "crispening" of the contours by inhibitory interaction can be made, using the eye of *Limulus*.[23] The discharge of impulses is recorded from a "test" receptor near the center of the eye as the eye is caused to scan slowly a pattern of illumination containing a gradient of intensity. When all of the receptors are masked except for the one from which activity is being recorded, a faithful representation is obtained of the distribution of intensity in the image viewed. But when the mask is removed, so that all of the receptors view the pattern, maxima and minima in the frequency of the test receptor discharge occur, corresponding to the regions bordering the gradient. These resemble in form and location the "Mach bands" seen by a human observer viewing the same pattern.

Interaction is known to take place in other sense organs. In the ear, von Békésy[24] has suggested that inhibitory interaction may be important in increasing pitch discrimination. Indeed, Galambos and Davis[25] have demonstrated inhibition of the activity of single auditory nerve fibers by tones differing in frequency from those used to excite the fibers. Also, von Békésy[26] has demonstrated "contrast" effects in the tactile stimulation of the skin, suggesting inhibitory interaction over considerable distances over the surface of the body.

In the higher nervous centers, integrative processes of great complexity take place. In the retina of the vertebrate eye, which—even though located in the peripheral sense organ itself—is nevertheless a nervous center of high order, there is an intricate interplay of excitatory and inhibitory interactions.[27] As a result, diverse and labile patterns of optical nerve fiber activity are generated.[28,29] In the vertebrate retina, to a much greater degree than in the primitive retina of *Limulus*, the patterns of afferent nervous activity are greatly modified to accentuate significant features of information about the environment. The process of neural integration is well begun by the time the afferent messages are transmitted to still higher centers in the brain.

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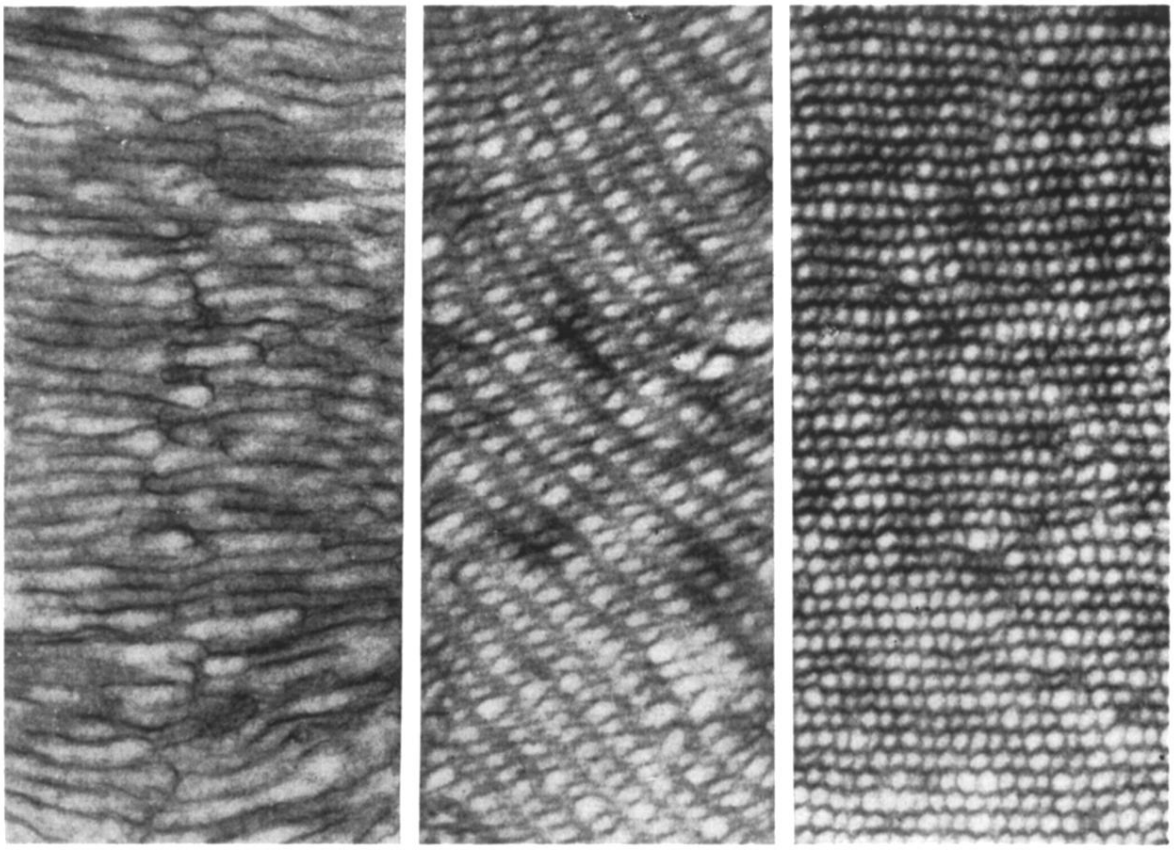


FIG. 1. Electron micrographs of rhabdom of an ommatidium of an arthropod compound eye (*Limulus*), showing honeycomb-like arrangement of osmium-staining membranes. Left: plane of section perpendicular to optical axis of ommatidium. Center: oblique section. Right: section in an axial plane. Height of figure approx 2 μ. Courtesy W. H. Miller.

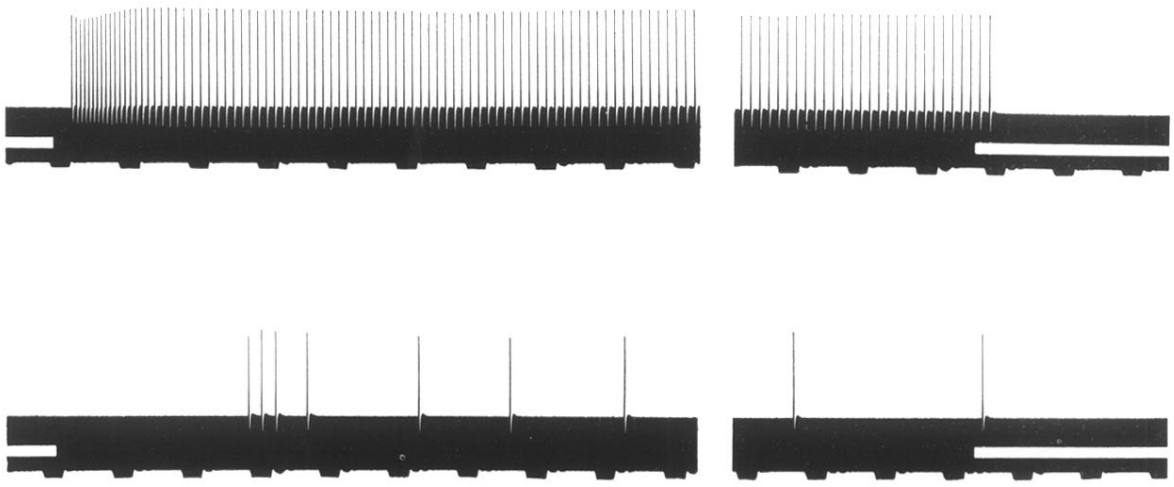


FIG. 2. Oscillograms of the electrical activity in a single optic-nerve fiber (eye of *Limulus*) in response to prolonged steady illumination of the facet of the eye innervated by the fiber.[15] Each spike is the "action potential" associated with the passage of a nerve impulse in the fiber. For the top record, the intensity of stimulating light was 10^4 times that used for the bottom record. Signal of exposure to light blackens out the white line above the time marks. Time marked in $\frac{1}{5}$ sec.

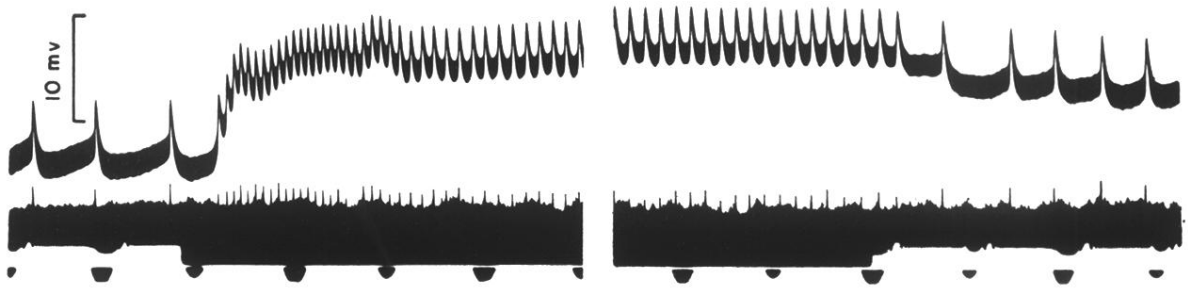
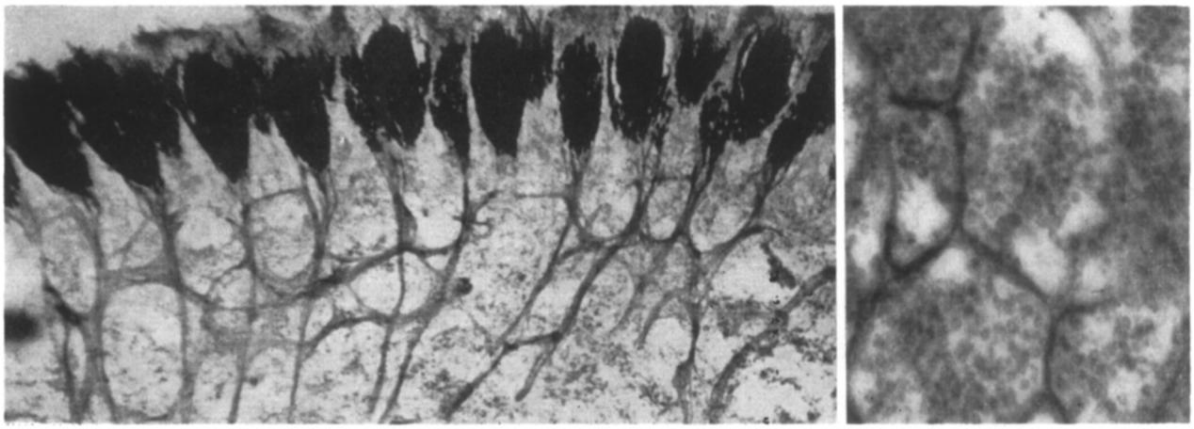


FIG. 3. Electrical responses to illumination of a single receptor unit (ommatidium) in the eye of *Limulus*.[15] Recorded (upper trace) by a micropipette electrode (tip diam 1 μ) in the neuron of the ommatidium, and simultaneously (black edge just below upper trace) by a pair of wire electrodes over which was slung the nerve bundle from the ommatidium containing the neuron's axon. At the beginning of the record, the microelectrode base line records the resting level of the electrical polarization of the cell membrane, at a potential about 50 mv negative to the solution bathing the outside of the cell. When the ommatidium was illuminated (black band above the time marks), there was a partial depolarization of the neuron (potential becoming less negative: rise in the base line) accompanied by an increase in the frequency of the spike-like deflections, each one of which was synchronous with the discharge of an impulse in the nerve bundle (small spikes on the black edge). Time marked in $\frac{1}{5}$ sec.



(a) (b)

FIG. 4. The plexus of the compound eye of *Limulus*. (a) Light micrograph of a section cut through the eye in a plane perpendicular to its external surface (cornea removed), showing on its upper border a row of the heavily pigmented ommatidia, from each of which emerges a small bundle of nerve fibers (stained with silver by Samuel's method) that contains, together with small fibers, the axon of ommatidium neuron. Connecting these bundles are festoons of fibers, with clumps of neuropile that appear at this magnification as condensations in the meshes of the plexus. Width of figure = 2.2 mm. Photograph by W. H. Miller [from H. K. Hartline, H. G. Wagner, and F. Ratliff, J. Gen. Physiol. **39**, 651 (1956)]. (b) Electron micrograph of a portion of a clump of neuropile in the plexus, showing a few outlines of the fibers composing the clump, within which are numerous small circular outlines interpreted as synaptic vesicles. Width of figure = 1.2 μ. Photograph by W. H. Miller.[19]

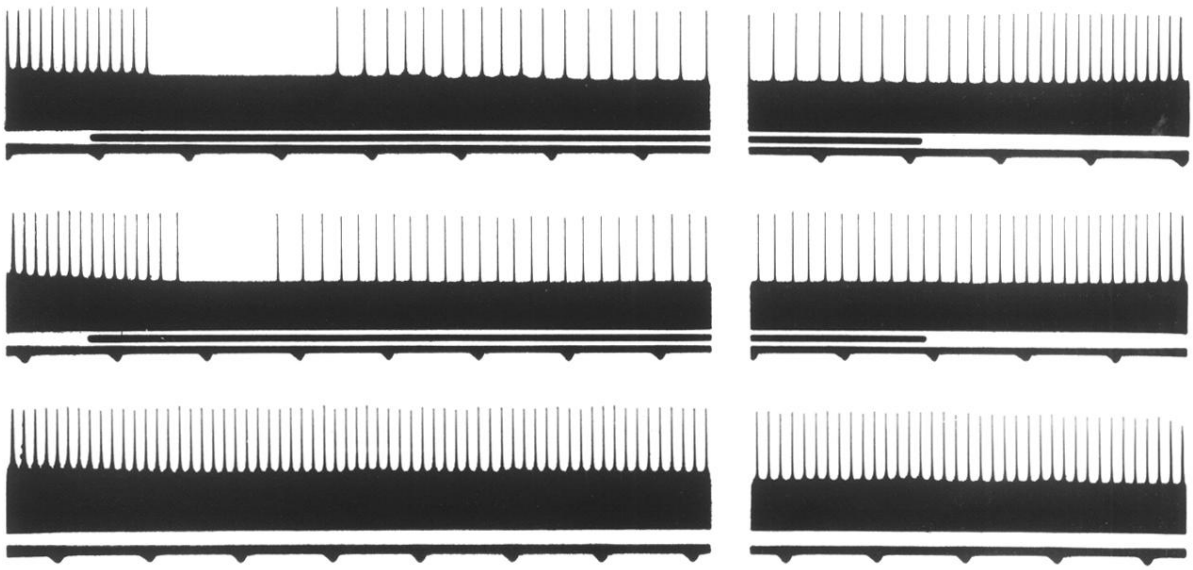


FIG. 5. Oscillograms of nerve action potentials, showing inhibition of the impulses in a single optic-nerve fiber of *Limulus*. The ommatidium of the eye from which the fiber arose was illuminated steadily at a fixed intensity, beginning 3 sec before the start of each of the records; adjacent ommatidium were illuminated during the interval signalled by the blackening out of the white line above the time marks, in the upper two records. In the top record, the intensity of the illumination of adjacent receptors was ten times that used in the middle record. Bottom record is a control (no adjacent illumination). Time in $\frac{1}{5}$ sec. Experimental arrangement as in Fig. 6(a).

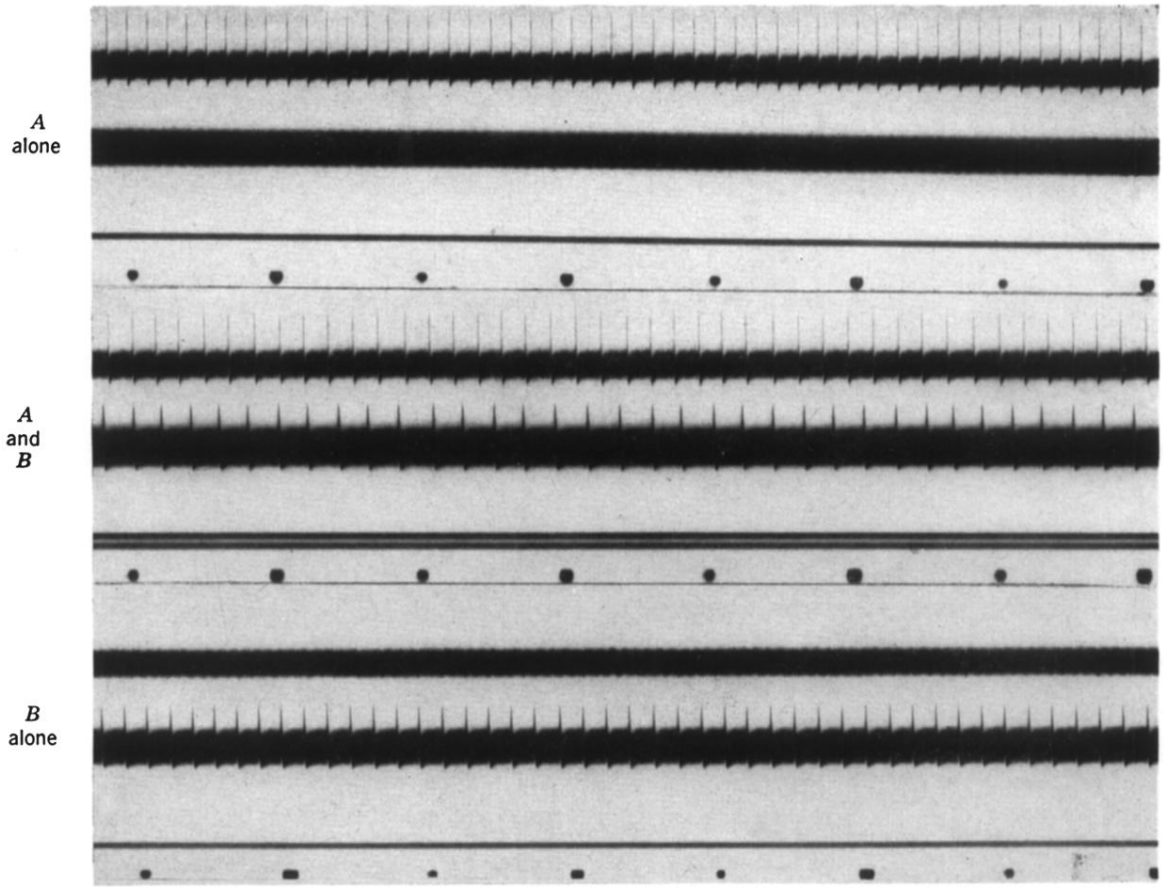


FIG. 7. Mutual inhibition of two ommatidia close to one another in the eye of *Limulus*, steadily illuminated at fixed intensity on each. Experimental arrangement as in Fig. 6(b). Time (black dots) in $\frac{1}{5}$ sec.