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THE NEURAL MECHANISMS OF VISION[1]

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OUR awareness of conditions in the external environment depends on the activity of our sense organs. These outposts of the nervous system signal the external conditions which affect the organism, translating environmental change into activity in sensory nerve fibers. It is then the function of the central nervous system to interpret this sensory information, integrating it into an appropriate pattern of behavior. The analysis of these complicated receptor and neural processes is the aim of sensory physiology.

A direct attack upon the problem of sensory mechanisms has been made possible by physical instruments for recording the minute and rapid electrical changes which accompany nervous activity. Thus the nerve messages from the sense organs can be intercepted. Furthermore, methods devised by Adrian and Bronk (1) for isolating single units from nerve trunks make it possible to record the activity in individual sensory nerve fibers. The analysis of visual mechanisms by these methods is the subject of this lecture.

The isolation of single fibers from the optic nerve, and the recording of their activity in response to illumination of the eye are accomplished by procedures now well known in electrophysiology. Small bundles of fibers dissected from the optic nerve are placed across electrodes in the input of an amplifier and their amplified action potentials recorded with an oscillograph. These bundles may be teased apart into fine strands, to the point where illumination of the eye elicits a regular sequence of uniform spike potentials, such as is recorded in Fig. 1. Such action potentials, it has been proved (1, 6, 33) are characteristic of the activity of single nerve fibers; they are the electrical sign of the

[1] Lecture delivered October 30, 1941.

regular trains of uniform impulses which constitute the nerve messages of the functional units of the nervous system.

The initiation of trains of nerve impulses by the action of light on the visual receptor cells is the first problem to be investigated by these methods. By the choice of a sufficiently primitive eye, in which the optic nerve fibers arise directly from visual sense cells, it has been possible to investigate the properties of the receptor mechanism in terms of the nervous activity it generates. The lateral eye of the horse-shoe crab, *Limulus*, provides a suitable preparation for this purpose (25), since the optic nerve fibers in this animal are the axones of the visual receptor elements themselves. The use of this preparation thus avoids the com-

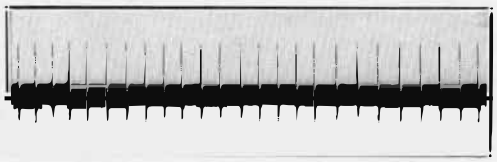


FIG. 1. Oscillogram of the amplified action potentials in a single optic nerve fiber (eye of *Limulus*) in response to steady illumination of the eye. Magnitude of deflection ca. 1 mv. Full length of record equals 1 second.

plexities introduced by the ganglionic structure of the vertebrate retina.

The simple sensory discharges recorded from the optic nerve fibers of *Limulus* resemble in their general properties nervous activity initiated by other kinds of receptors. The manner in which intensity of stimulation affects the discharge of nerve impulses provides an example. The relation between the intensity of illumination of the receptor and the resulting sensory discharge is shown in the records of Fig. 2. The higher the intensity of light falling upon this receptor cell, the greater was the frequency of impulses discharged in its optic nerve fiber. The individual nerve impulses, of course, were not graded in size (in keeping with the well known "all-or-nothing" property of nerve fibers); nevertheless, the receptor cell was able to signal different intensities of illumination by different frequencies of its sensory

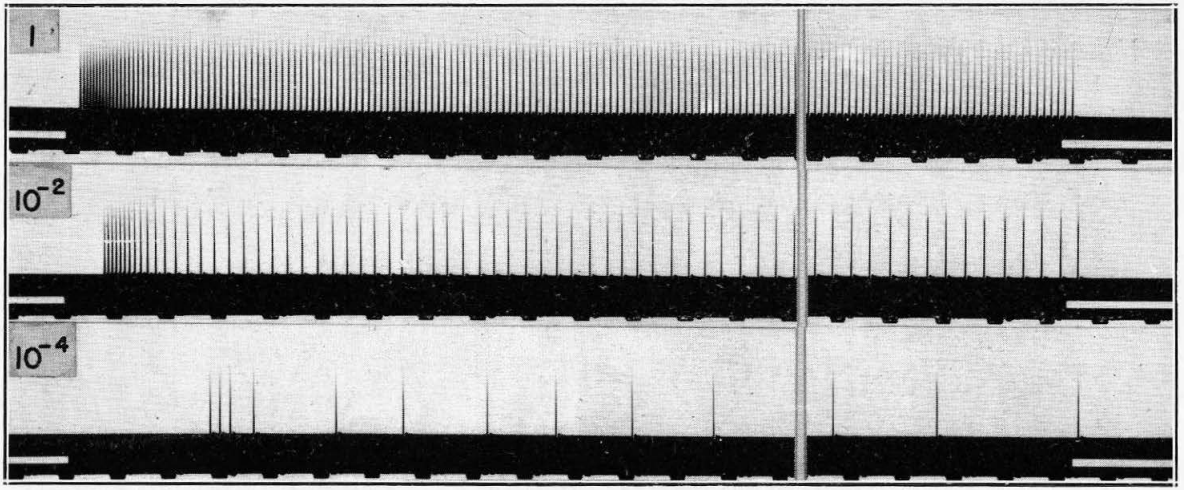


FIG. 2. Discharge of impulses in an optic nerve fiber (eye of *Limulus*) in response to illumination of the eye at three different intensities (relative values given at left). Eye partially light adapted. Signal of exposure to light blackens out white line above time marker. Time marked in 1/5 sec.

discharge. This is how intensity of stimulus is mediated by the individual sensory elements. Not only the visual receptor cells, but all the other sensory endings which have been studied by of stimulus by altering the frequency of the sensory discharge these methods show this same mechanism of signaling intensity (5, 6, 10, 32, 33, 34, 35).

Another property of the visual sense cell which it shares with other kinds of receptors is also shown in Fig. 2. At the onset of illumination of each intensity, the discharge of impulses began

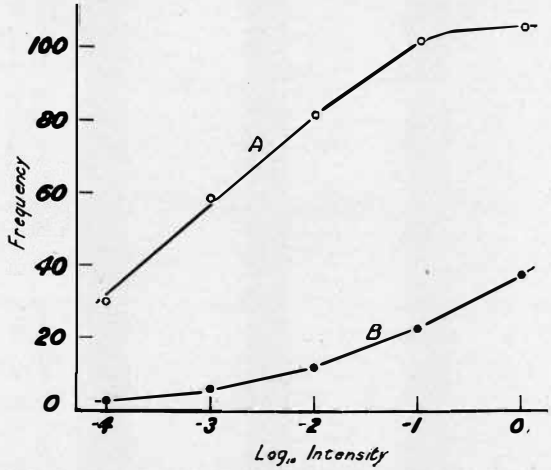


FIG. 3. Relation between frequency of impulses (number per record) and logarithm of intensity of stimulating light for the discharge in a single optic nerve fiber (eye of *Limulus*). Curve A, frequency of initial maximal discharge. Curve B, frequency of discharge 3.5 sec. after onset of illumination (Hartline and Graham (25)).

at a high frequency which declined, at first rapidly, then more slowly, approaching a steady level which was maintained as long as the light continued to shine. Such sensory adaptation is exhibited to a greater or less degree by all kinds of receptors thus far studied. Subjectively, it is common experience that a light when first turned on appears considerably brighter than after it has been shining several seconds. We have no absolute gauge of the intensity of a light, and this we may ascribe directly to the

property of sensory adaptation of the receptor elements of our retinas, which furnish no fixed single value of impulse frequency corresponding to a particular absolute intensity of illumination.

Adaptation of the visual receptor, nevertheless, has useful functions. Not only does it serve to emphasize sudden changes in conditions of illumination, but it extends the range of intensities which a single receptor can mediate. Fig. 3 shows graphically the variation of frequency of discharge in a single optic nerve fiber with intensity of illumination. Curve A gives the values for the initial maxima of the sensory discharges, Curve B the values of the frequencies after 3 sec. of continuous illumination. At high intensities curve A tends to flatten out, and would ultimately be limited by the inability of the receptor to generate such high frequencies, or of the nerve fiber to follow; after adaptation to these high intensities, however, the receptor, as shown by Curve B, is able to give a significant variation of frequency with intensity. Thus each individual visual sense cell combines a high sensitivity with a wide range of response.

The mechanism whereby light energy is translated by the receptor cell into nervous activity is as yet far from being understood. However, it is clear that the initial step in this process must be the absorption of light by a photosensitive substance in the sensory cell. The resulting photochemical reaction is then the first step in the excitation of the receptor. Only light that is absorbed can be effective in initiating a photochemical reaction, and since photosensitive substances do not in general absorb all wavelengths equally, it follows that different wavelengths will have different effectiveness in exciting the visual sense cell. In Fig. 4 are shown records of the activity of a single optic nerve fiber whose receptor was stimulated by brief flashes of light of various wavelengths. The different spectral lights were not equally effective, and in order to produce equal responses of the sense cell (measured in terms of number of impulses discharged in its optic nerve fiber) it was necessary to adjust the relative energies of the flashes of different wavelengths to the values given in the figure. The receptor was less sensitive to red and

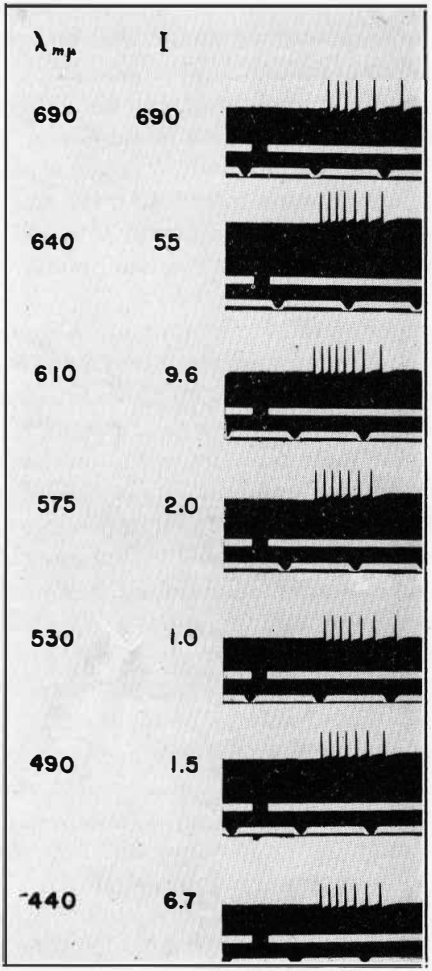


FIG. 4. Discharges of impulses in a single optic nerve fiber (*Limulus*) in response to lights of different wavelengths (λ), showing that responses can be made practically identical by suitable adjustment of the incident intensities (I). Values of I (thermopile determinations) are given relative to its value at $\lambda = 530$ mμ. Duration of stimulus flash 0.04 sec., signaled in the white line above time marker. Time in 1/5 sec. (Graham and Hartline (14)).

violet light than to green; the "visibility curve" plotted from these measurements (Fig. 5) may be simply interpreted as the absorption spectrum of the photosensitive substance of the visual sense cell (14, 15, 18, 30).

The comparatively simple nature of the primary photochemical reaction in the visual sense cell is indicated by the responses to short flashes of light of various intensities and durations (19).

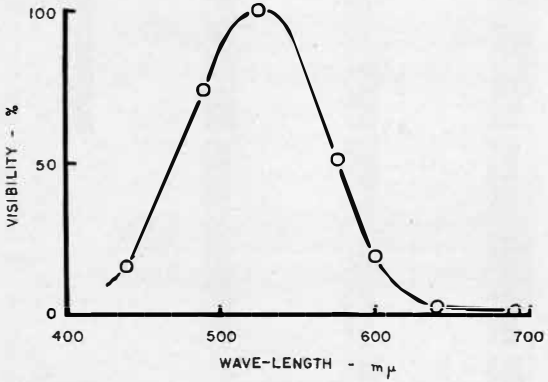


FIG. 5. Visibility curve for a single visual sense cell (*Limulus*). "Visibility" at each wavelength is the reciprocal of the relative intensity necessary to produce a specified burst of impulses (cf. Fig. 4) (data from Graham and Hartline (14)).

Fig. 6 is an array of records of the responses of a single optic nerve fiber, showing that both the intensity and the duration of the stimulating flash affect the latency of the response, the number of impulses discharged and the frequency of the discharge. These two parameters of the stimulus indeed affect the response of the sense cell to the same degree quantitatively, as may be seen by an inspection of the figure. The recorded responses which stand in any given diagonal of this array (upper left to lower right) are very closely equal; for each of these responses the energy of the stimulating flash (product of intensity by duration) was the same. Apparently the photochemical reaction which is the first step in the excitation of the receptor is sufficiently simple so that the reciprocity law of photochemistry applies to it, provided only short durations of exposure are considered.

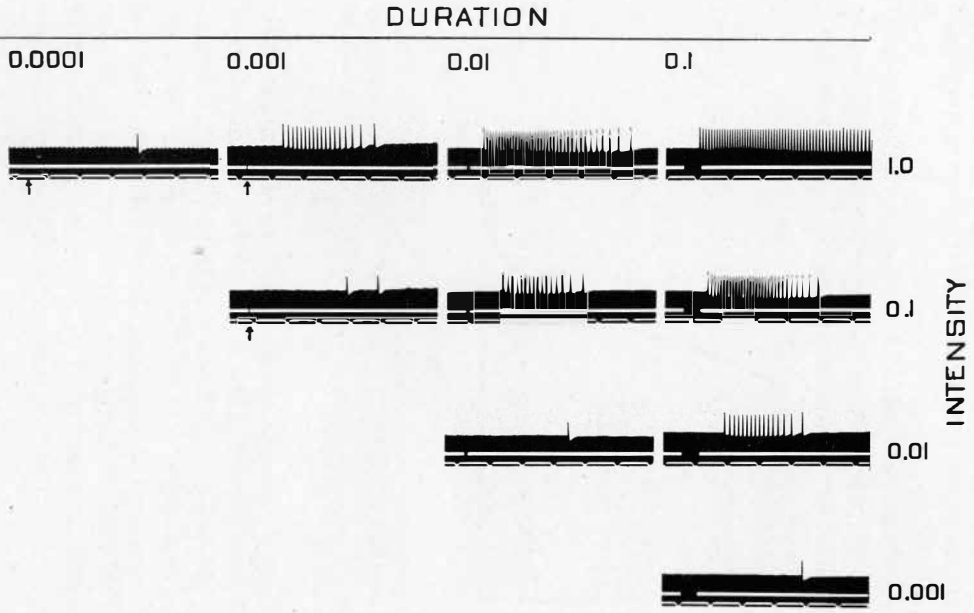


FIG. 6. Discharges of impulses in a single optic nerve fiber (*Limulus*) in response to short flashes of light of various intensities and durations. Relative intensity for each horizontal row given on right. Duration of flash (in seconds) for each vertical column given at top. Signal of light flash blackens the white line above time marker (arrows mark position of signal for very short flashes). Time in $\frac{1}{2}$ sec. (Hartline (19)).

The photochemical change produced by light necessarily results in a depletion of the photosensory substance of the sensory cell, with a consequent fall in its sensitivity. This undoubtedly

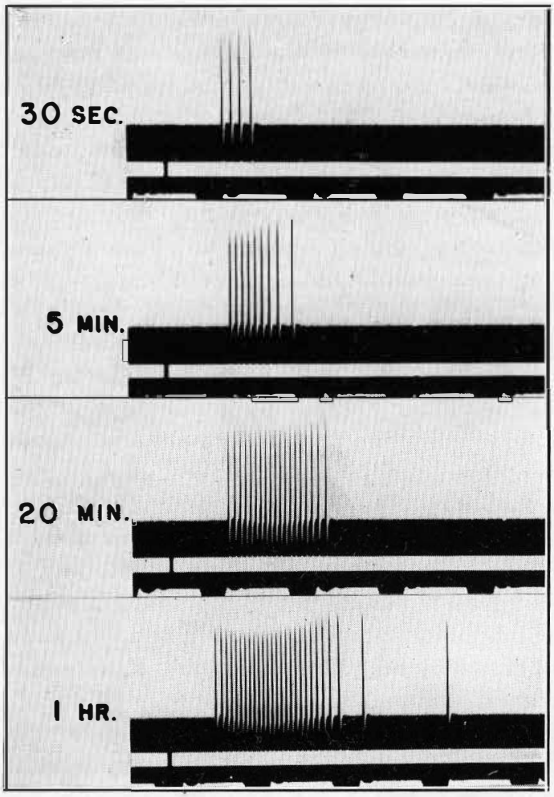


FIG. 7. Dark adaptation of a visual sense cell. Discharges of impulses in an optic nerve fiber (*Limulus*) in response to a test flash of light (0.01 sec., fixed intensity) at various times (given at left) following an adapting exposure. Signal of flash appears in white line above time marker. Time in 1/5 sec. (Hartline and McDonald, in preparation).

is the explanation, in part, of the "sensory adaptation" described above. It is to be noted, however, that the discharge (Fig. 2) does not subside completely, but reaches a steady level at which

impulses continue to be discharged as long as light shines on the eye. Evidently there are restorative processes in the sense cell which can maintain the supply of photosensitive material even in the face of active photolysis. A stationary state is reached when the rate of the restorative reaction equals that of photolysis (28); its level depends upon the intensity of illumination, and in turn determines the frequency of the discharge of impulses in the nerve fiber.

Following a period of exposure to light the restorative reaction proceeds unopposed by photolysis, and as the photosensitive material accumulates the receptor cell recovers its original sensitivity in the process of dark adaptation. This may be measured by recording the discharge of impulses in response to a test flash of constant intensity thrown upon the eye at various times following exposure to an adapting light (26). Records from such an experiment are shown in Fig. 7. Immediately after the adapting exposure the flash could elicit only a few impulses, but as dark adaptation proceeded, the responses to the flash became greater and greater, until the receptor had completely recovered its original sensitivity. The course of dark adaptation following various amounts of preceding light adaptation is shown graphically in Fig. 8. The greater the intensity of the pre-adapting exposure, the greater was the initial depression of sensitivity, and the slower the subsequent recovery. Curves revealing similar changes in sensitivity are characteristically obtained in studies of human dark adaptation (27, 31, 37).

These reactions of photolysis and regeneration of photosensitive materials are not purely hypothetical; chemical studies of photosensitive substances which can be extracted from the eyes of vertebrates furnish a sound basis for our understanding of the photochemical mechanism of the visual receptor. Not only can the photosensitive substances and their photoproducts be identified chemically, in some cases, but the photochemical reactions and the recombination of the photoproducts may be observed *in vitro* (12, 29, 36). Thus the first step in the excitation of the visual sense cell is beginning to be understood. On the other

hand, very little is known about the processes intermediate between the initial reaction and the final discharge of nerve impulses (20). This problem, however, is not confined to the visual sense cell; it is part of more fundamental questions concerning the excitation of nerve cells of any kind, and the mechanisms whereby they initiate trains of impulses in their fibers (9, 11). It is to be hoped that recent studies on the origin of trains of impulses from chemically treated regions of peripheral nerve fibers will aid in the understanding of this fundamental mechanism of the sense cell (7, 8, 13).

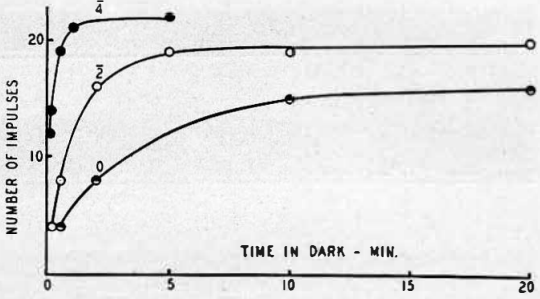


FIG. 8. Recovery of sensitivity of a single visual sense cell (*Limulus*) during the dark adaptation following various intensities of light adaptation. Ordinates give number of impulses discharged in response to test flash of fixed energy; abscissae give time in minutes after the end of the 10 sec. period of exposure to light. Numbers on the curves gives the logarithm of the relative intensities of the adapting light. (Hartline and McDonald, in preparation).

In a study of visual mechanisms it is not enough to limit one's attention to the properties of the isolated visual sense cells. The eye comprises many sensory elements, differing in their individual properties and varying in their responses with the degree and kind of illumination upon them. It is the aggregate of the diverse sensory messages arising from all the receptor elements that the visual centers must integrate. Thus the sensory elements of our retinas are spread in a mosaic to receive the retinal images of different external objects. In *Limulus*, different facets point in different directions to accomplish, crudely, a

similar effect. Fig. 9 shows records obtained from a preparation in which the nerve strand happened to contain two active fibers, coming from receptor cells in different facets of the eye. Because of local differences under the recording electrodes the different fibers gave rise to spike potentials of different heights; it is consequently easy to distinguish activity in the separate fibers. The figure shows how illumination of one or the other or both facets resulted in corresponding activity in one or the other or both nerve fibers (25). This is so elementary as to be almost

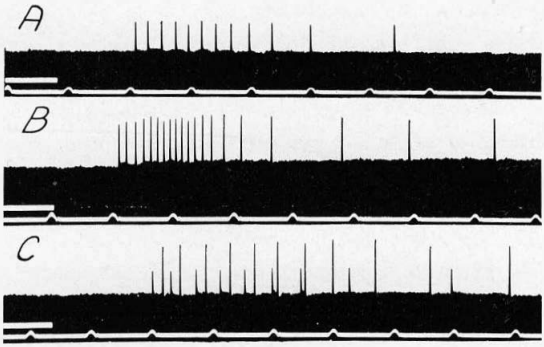


FIG. 9. Action potentials of two optic nerve fibers from two separate facets of the eye of *Limulus*. A. Discharge in response to illumination of the first facet alone. B. Discharge in response to illumination of the second facet alone. C. Discharge in response to illumination of both facets together. Signal of illumination above time marker. Time in 1/5 sec. (Hartline and Graham (25)).

trivial, yet it is the basic sensory information which enables the animal to distinguish visual form and pattern.

Not only can the distribution of light and shade in the retinal image be recognized but many of the higher animals can distinguish the color of light as well. It was pointed out above that lights of different wavelengths have different degrees of effectiveness in exciting the visual sense cell of *Limulus*. However, once the energy of the incident light is adjusted to compensate for this difference in effectiveness, the responses to different colored lights are identical; there is nothing in the discharge of impulses by an individual sense cell to distinguish what wavelength is

used to excite it. It is not known whether *Limulus* can distinguish colors, but even in animals known to possess color vision we would hardly expect any other result from a study of their isolated receptor cells. Different qualities of the stimulus are probably mediated not by individual sensory elements, but by the aggregate of them. Different receptor cells, possessing different spectral distributions of sensitivity, are usually supposed to furnish the peripheral basis for color discrimination. It is in-

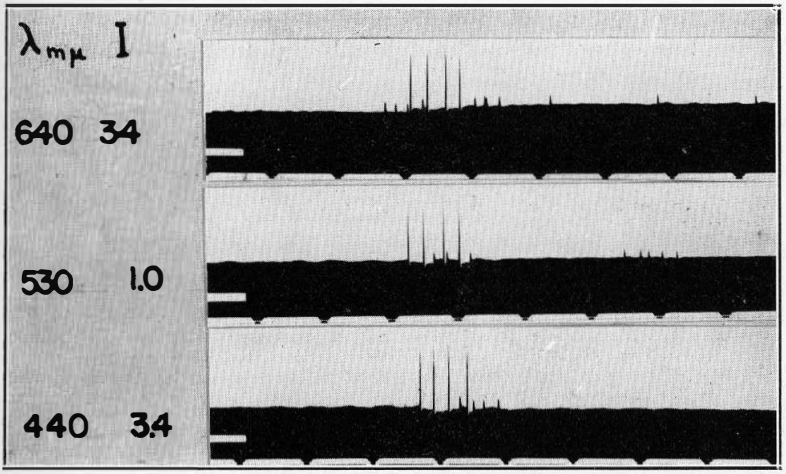


FIG. 10. Action potentials of two optic nerve fibers (*Limulus*) in response to lights of different wavelengths (λ). Relative intensities (I) adjusted to elicit 4 impulses in fiber giving large spikes; these intensities are not equally effective for the fiber giving the small spikes. Signal of illumination above time marker. Time in 1/5 sec. (Graham and Hartline (14)).

teresting that even the primitive eye of *Limulus* possesses this much of a possible color vision mechanism. In Fig. 10 the activity in two optic nerve fibers from two sensory elements, closely adjacent in the eye, can be recognized by characteristic differences in height of the spike potentials. The three spectral lights used were adjusted to produce equal responses (4 impulses) in the fiber yielding the large impulses. It is seen that this does not

constitute a match for the other fiber, whose receptor cell was relatively more sensitive to the red end of the spectrum. While neither sense cell, acting alone, could signal the wavelength of the light, it is evident that the information provided by both together could be used by the animal to distinguish one end of the spectrum from the other (14). To make use of this sensory information the animal must possess the adequate central mechanisms for integrating this kind of pattern of nerve fiber activity. Recent studies by Granit (16, 17) on neurons of the vertebrate retina have shown that differential sensitivity to lights of different wavelengths is well developed in animals possessing the ability to discriminate color.

The properties of the higher neurons in the visual pathway, whose function it is to integrate the various patterns of receptor activity, may be analyzed ultimately by methods similar to those we have just described. To make a beginning in this analysis the vertebrate eye has been chosen since the axons of the retinal ganglion cells are accessible as the fibers of the optic nerve. The retinal ganglion cells are the third neurons in the chain, counting the receptor elements (rods and cones) as the first, and it is not surprising to find that their activity is considerably more complicated than the simple sensory discharges of the visual sense cells of *Limulus*. The discharge of impulses in the vertebrate optic nerve was first studied by Adrian and Matthews (2, 3, 4); the experiments to be described are an extension of their studies to an investigation of the properties of the individual retinal neurons.

A slightly different procedure is necessary to record the discharge of impulses in single optic nerve fibers from the vertebrate eye (21). The eye of a frog or other cold-blooded vertebrate is removed and opened, and its cornea, lens and vitreous humor are removed, exposing the retina. The optic nerve fibers form a thin layer on the surface of the retina, and small bundles of them may be dissected from the retina in the region where they converge to the head of the optic nerve. Such a bundle, split until only a single nerve fiber remains active, may be placed on

electrodes and its electrical activity recorded in the usual manner. The retina is then explored with a small spot of light to determine the region which must be illuminated in order to elicit a discharge of impulses in the fiber. Recently micro-electrodes have been devised which when inserted in the retina record the activity from a very few retinal neurons, and records have been published which show clearly the activity from single ganglion cells (16, 18, 38, 39; cf. also Fig. 12). This method has made it possible to extend these studies to the mammalian retina.

The most striking feature of the activity of vertebrate optic nerve fibers wherein they differ from simple sensory discharges, is the wide diversity of the responses of different fibers. Fig. 11 shows the three principal types of response observed in single optic nerve fibers from the eye of the frog. In some of the fibers (Fig. 11 A) the discharge is similar to that from a simple receptor cell: impulses are discharged regularly as long as the light shines. Other fibers (Fig. 11 B) discharge impulses only briefly, when the light is turned on and again when it is turned off, showing no activity whatever as long as the light shines steadily. The "off" responses in these fibers are a marked departure from simple sense-organ activity. Even more remarkable are the fibers whose only response occurs when the light is turned off (Fig. 11 C). These different kinds of response are not due to different conditions of stimulation or adaptation of the retina; a given optic nerve fiber has its fixed pattern of response, and fibers with different types of response can be found in the same bundle of fibers, coming from closely adjacent regions of the retina. These same types of response are commonly met in all the cold-blood vertebrates that have been studied and have also been reported from the retinas of mammals (16, 39).

There is no certain explanation for this diversity of response among the optic nerve fibers of the vertebrate eye. It does seem reasonable, however, to ascribe it to the complex ganglionic structures of the retina intervening between the sensory receptors and the axons of the retinal ganglion cells. Moreover, direct evidence has been obtained that ganglionic structures are capable of

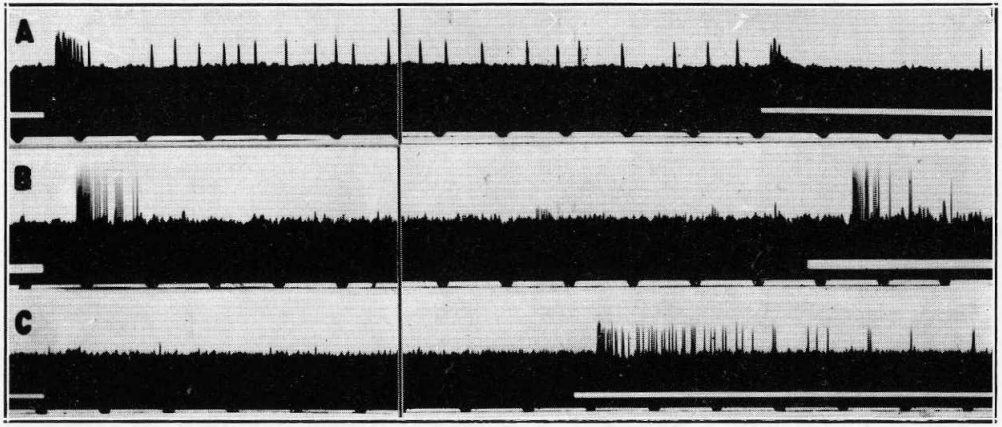


FIG. 11. Oscillograms of the action potentials of single optic nerve fibers of the vertebrate eye (frog) illustrating the three most common types of response to illumination of the retina. Signal of the retinal illumination blackens the white line above the time marker. Time in 1/5 sec. (Hartline (21)).

modifying the simple sensory discharge, and so give rise to quite different patterns of response. This has been shown in the optic ganglion of *Limulus*, by the use of micro-electrodes for recording the activity of single neurons (40). We have already described the activity in the optic nerve fibers of *Limulus*, and in the hundreds of preparations we have studied not a single case has been found of anything but the simple discharge of impulses during illumination of the eye. When the optic lobe of the central ganglion is explored, however, activity of neurons has been recorded in which the discharge of impulses occurs only in response to cessation of illumination upon the eye (Fig. 12).

FIG. 12. Action potentials recorded by micro-electrodes in the optic ganglion of *Limulus*. Upper record, responses to illumination of the eye recorded by a large electrode inserted in the ganglion at the point of entrance of the optic nerve. Lower record, responses to illumination of the eye recorded by a small electrode inserted in the same ganglion approximately 2 mm. posterior to the point of entrance of the optic nerve. Signal of illumination above time marker. Time in 1/5 sec. (Hartline and Wilska, in preparation).

These responses can be elicited equally well by electrical stimulation of the central end of the optic nerve, and occur only upon the cessation of stimulation. In all their properties these "off" responses found in the *Limulus* optic ganglion resemble the pure "off" discharges observed in the vertebrate retina (Record C of Fig. 11).

The same factors which have been shown to determine the

responses of the visual sense cells in the eye of *Limulus* likewise affect the discharge of impulses in the vertebrate optic nerve fibers. Thus the frequency of the discharge is greater the higher the intensity of the retinal illumination; likewise the sensitivity of the retina is diminished by light adaptation and recovers as the eye is allowed to remain in darkness. In addition, certain new properties emerge. The fibers responding with short bursts of impulses at the onset and cessation of illumination also respond even to slight changes in intensity—the greater the change the stronger the response. These fibers are also extremely sensitive to movements of the retinal image, whether it be a spot of light or a small shadow on the uniformly illuminated retina (Fig. 13). The higher the intensity, and the more rapid and extensive the movement, the greater the number of impulses discharged in response. The importance of this type of discharge to the animal is obvious.

The discharge of impulses in fibers which respond only to turning the light off usually subsides in a second or two; the initial frequency and the duration of this discharge are greater the higher the intensity and the longer the duration of the preceding exposure. Thus the "off" responses are strictly dependent on the preceding illumination, although these ganglion cells discharge no impulses during the period when their excitation is being built up. Indeed, the discharge in these fibers can be abruptly suppressed at any time merely by re-illumination of the retina (Fig. 14). The "off" responses from the *Limulus* ganglion have these same properties. Thus in the visual system there are neurons whose activity is governed by inhibitory as well as excitatory influences, and the interplay of excitation and inhibition which is characteristic of central nervous activity is a prominent feature of retinal function.

The detailed analysis of the integration of sense cell activity by the higher neurons is a formidable problem, and one that may be more suitably attacked elsewhere than in the visual pathway. Nevertheless it is possible to show how some of the fundamental principles of central nervous function govern the activity of neurons in the visual system.

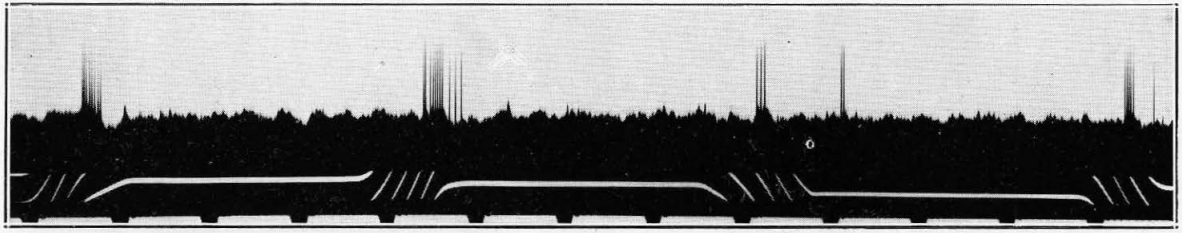
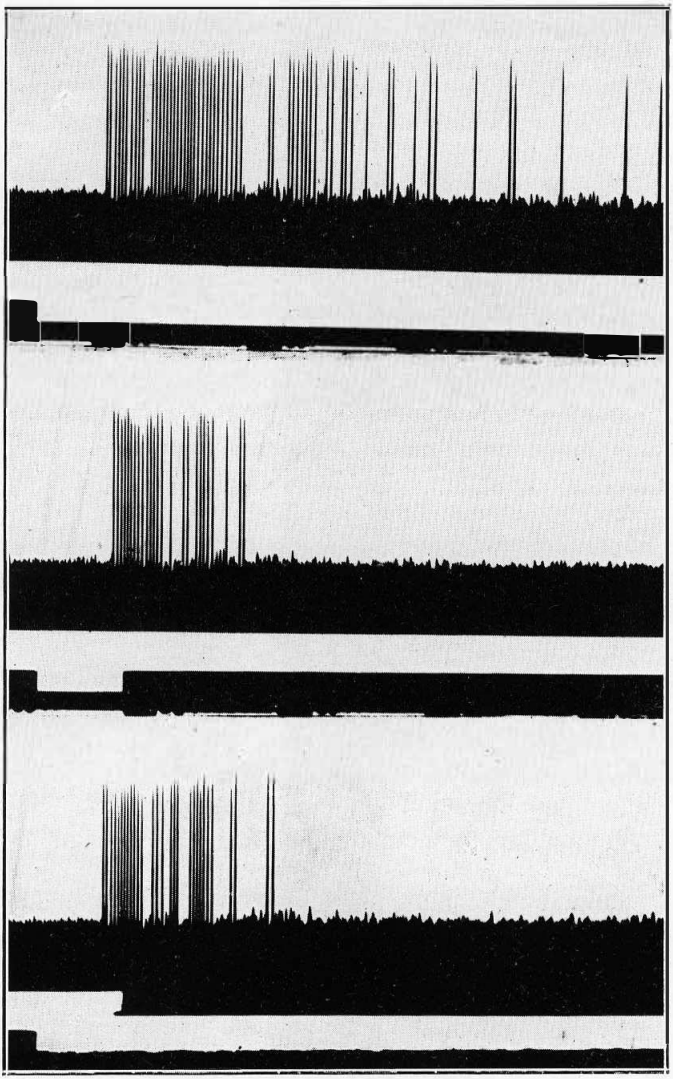


FIG. 13. Bursts of impulses discharged in an optic nerve fiber (frog) in response to movement of a small spot of light (50 μ diameter) on the retina. White lines above time marker signal the movement; each stroke corresponds to a movement of 7 μ on the retina. Time in 1/5 sec. (Hartline (23)).



It is well known that the receptor elements of the vertebrate eye greatly outnumber the retinal ganglion cells, and that each ganglion cell in the peripheral retina makes connection with many retinal rods (through the intermediate bipolar cells). It is therefore not surprising to find that a single retinal ganglion cell can be excited by light falling anywhere within a retinal area which, although small, has appreciable extent, and must comprise many receptor elements (23). The retinal region occupied by visual sense cells whose connections converge upon a given retinal ganglion cell shall be termed the receptive field of that ganglion cell. The extent and the distribution of sensitivity within the receptive fields of ganglion cells has been charted by exploring the retina with a small spot of light while recording the activity in single optic nerve fibers. In Fig. 15 a are plotted the contours of the area within which a spot of light elicited a discharge of impulses in an optic nerve fiber from the peripheral retina of a frog's eye. Two intensities of exploring spot were used; the less intense one could elicit responses only when it fell within the more sensitive central portion of the fiber's receptive field. Fig. 15 b shows, in another experiment, the contours for three different intensities of exploring spot. These experiments show that sensitivity to light, for a particular ganglion cell, is not uniformly distributed over the whole retina. The region of maximal sensitivity is usually at least several tenths of a millimeter in diameter, but responses to light can be elicited over a considerably larger region; appreciable sensitivity generally extends over an area of approximately one square millimeter.

FIG. 14. Inhibition of the "off response" (frog optic nerve fiber) by re-illumination of the retina. Upper record: discharge of impulses in response to cessation of illumination (cf. Fig. 11 C). Short black strip appearing on lower edge of white band (above time marker) signals the retinal illumination by the spot of light giving rise to this off response. Middle record: "Off response" cut short by re-illumination of the same spot of light (black strip is interrupted during the brief interval of darkness). Lower record: "Off response" is cut short by illumination of an adjacent spot of light (0.2 mm. removed), signalled by black strip on upper edge of white band. Time in 1/5 sec. (Hartline, in preparation).

Not only do excitatory influences converge upon each ganglion cell from different parts of its receptive field, but in the case of ganglion cells giving pure "off" responses, inhibitory influences converge as well. Fig. 14 shows "off" responses which have been abruptly cut short by re-illumination of the retina. In the middle record the re-illumination was applied to the same retinal area as the initial (exciting) illumination; in the lower record

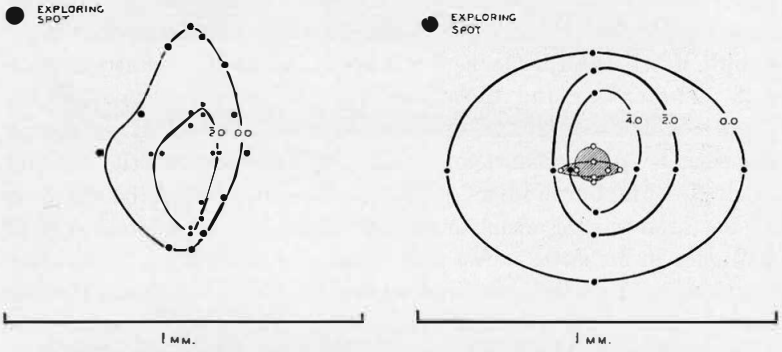


FIG 15. Charts of the retinal regions supplying single optic nerve fibers (eye of the frog). a. Determination of the contours of the receptive field of a fiber at two levels of intensity of exploring spot. Dots mark positions at which exploring spot (50 μ in diameter) would just elicit discharges of impulses, at the intensity whose logarithm is given on the respective curve (unit intensity = 2.10^4 meter candles). No responses at log I = − 3.0, for any location of exploring spot. This fiber responded only at "on" and "off." b. Contours (determined by four points on perpendicular diameters) of receptive field of a fiber, at three levels of intensity (value of log I given on respective contours). In this fiber steady illumination (log I = 0.0 and − 2.0) produced a maintained discharge of impulses for locations of exploring spot within central shaded area; elsewhere discharge subsided in 1–2 seconds. No maintained discharge in response to intensities less than log I = − 2.0; no response at all to an intensity log I = − 4.6. (Hartline (23)).

it was applied to an area 0.2 mm. away from the initial spot, but still within the receptive field of the fiber. The efficacy of a spot of light in inhibiting an "off" discharge is greatest if it falls in the center of the receptive field; the less sensitive margins require more intense illumination to produce the same degree of inhibition (22).

Where there is convergence of neural pathways it is not surprising to find spatial summation. This is a property of the vertebrate retina which has been clearly demonstrated by the work of Adrian and Matthews (2, 3, 4). Spatial summation of excitatory effects is most simply shown in the influence of the area of the retinal illumination upon the discharge of impulses in a single optic nerve fiber (24). Fig. 16 shows the responses to

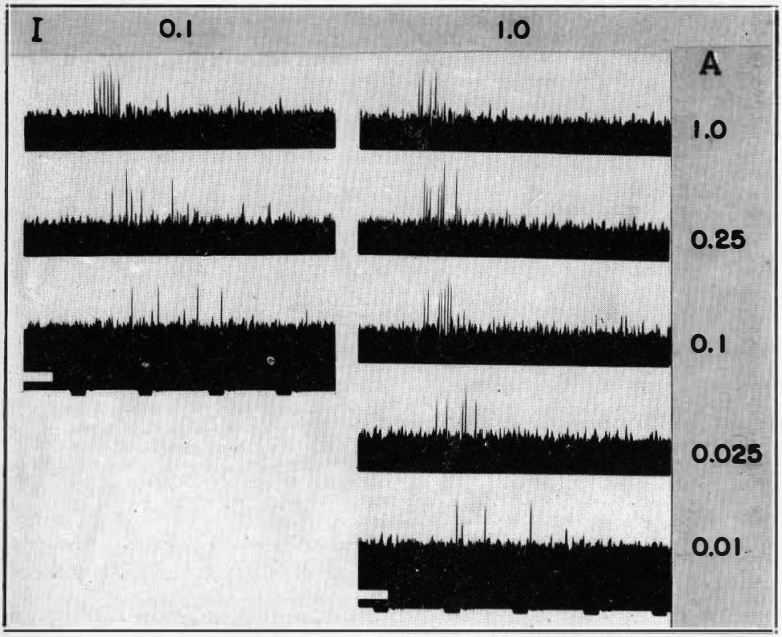


FIG. 16. Oscillograms of action potentials in a single optic nerve fiber from a frog's retina, showing effect of size of stimulus patch upon the discharge of impulses. Retina illuminated with circular patches of light, centered on receptive field of the fiber; relative areas (A) given on right (A = 1 corresponds to 0.006 mm.^{2}). For the responses in the left hand column the intensity of illumination was 1/10 that used for the right hand column. (I = 1 equivalent to 3.10^5 meter candles). Fiber was one responding with bursts of impulses at "on" and at "off" with no impulses discharged during steady illumination. Only "on" burst shown here. Signal of illumination blackens white line above time marker (only shown in bottom records). Time in 1/5 sec. (Hartline (24)).

illumination of the retina with patches of light of various sizes falling well within the limits of the fiber's receptive field. The larger the area illuminated by a stimulus patch of fixed intensity the shorter was the latency of the response, and, for moderate degrees of stimulation, the higher was the frequency and the greater the number of impulses in the discharge. These effects are similar to those obtained by increasing the intensity of a

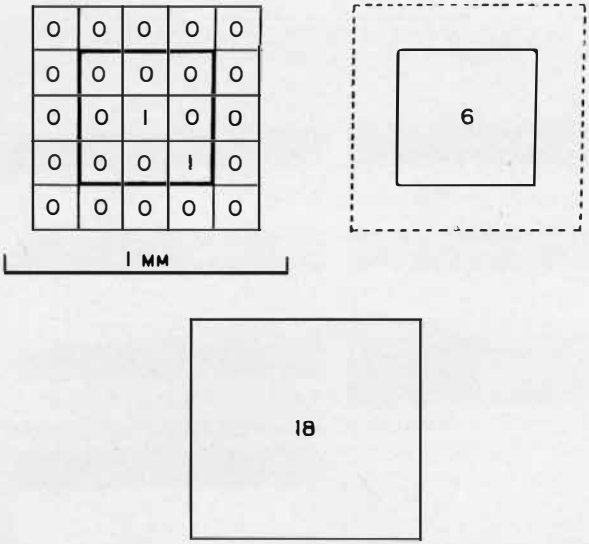


FIG. 17. Chart showing the responses of a single optic nerve fiber (frog eye) to illumination of different portions of its receptive field, at a fixed intensity (2.10^{-3} meter candles). Upper left: number of impulses in response to each of 25 subdivisions of large square, tested individually (comparative scale given below). Upper right: response to illumination of area covered by 9 central subdivisions (heavy outline in upper left). Below: response to illumination of entire square. Fiber responded only to "off." Duration of exposure for each test ca. 5 sec. (Hartline (24)).

patch of light of fixed area, as may be seen from a comparison of the responses in the two columns of Fig. 16 (obtained at two different intensities). Indeed, it is only the total amount of luminous flux (area × intensity) that determines the response of the ganglion cell. This relation holds only provided the area

illuminated does not include the less sensitive marginal regions of the fiber's receptive field, which can contribute only a little to the excitation of the ganglion cell. With large areas which exceed the size of the receptive field only the intensity of illumination determines the response.

To show the relative contributions of different elements of area to the total excitation of the ganglion cell the responses to illumination of subdivisions of a retinal region may be compared with each other and with the responses to illumination of the entire area. Such experiments show that the threshold intensity for a given area is lower than the threshold for its most sensitive subdivision; it is the total number of convergent pathways activated that determines the response in the final common pathway. Fig. 17 shows a chart of the number of impulses obtained in response to illumination of a retinal area and its subdivisions. The intensity was so chosen that none of the smallest subdivisions when illuminated alone could elicit a response in the optic nerve fiber with the exception of two, each of which could elicit only one impulse. Yet when the nine most central subdivisions were illuminated together at this same intensity the ganglion cell responded with six impulses, and when all 25 subdivisions were illuminated a burst of 18 impulses resulted. Evidently the separate retinal pathways can be excited to a degree which is subliminal for the ganglion cell, but when several convergent pathways act together their effects can sum to produce a discharge of nerve impulses. The summation of subliminal effects indicates that more than one nerve impulse in the retinal pathways must impinge upon the retinal ganglion cell to produce even a single impulse in its axon.

If the retinal illumination is made intense enough even a very small subdivision of the receptive field of a fiber will elicit a discharge of impulses. When several such subdivisions are illuminated together, spatial summation takes place and the excitation of the ganglion cell is greater than that produced by the most effective subdivision acting alone. Fig. 18 is a chart showing the frequencies of discharge in a fiber in which activity

was maintained throughout a steady illumination. The frequency of discharge in response to illumination of the large area was higher than the highest frequency obtained by illumination of any one of the nine subdivisions of this area. Fig. 19 shows the records of the discharge due to illumination of the total area and that due to its most effective subdivision. The retinal ganglion cell is the final common path for sensory activity originating in many receptor elements; its excitation is determined by the summation of all the excitatory influences reaching it over the pathways which converge upon it.

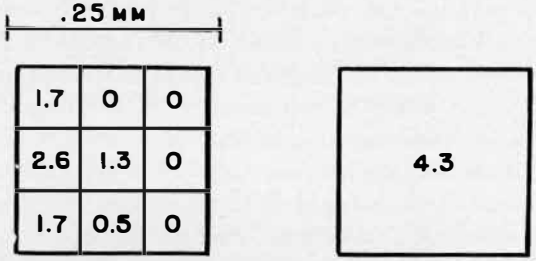


FIG. 18. Chart showing the response of a single optic nerve fiber (frog eye) to illumination of different areas in its receptive field. Discharge in this fiber was maintained during steady illumination; numbers give the frequency of this discharge in response to illumination of each of the 9 small squares (left) compared with the response to illumination of the entire area covered by these squares (right). Scale of retinal distances given above. (Hartline (24)).

Because of the spatial summation taking place in the peripheral retina we are enabled to see dimly illuminated objects which would otherwise be invisible, provided they are large enough. This sensitivity, however, is achieved at the expense of visual resolution; we cannot distinguish fine detail in the periphery of our visual field. It is recognized that this poor resolution is due to the large number of sensory elements corresponding to each ganglion cell in the peripheral retina. These experiments have shown how illumination falling anywhere within the receptive field of a single ganglion cell can cause its excitation. Moreover, the receptive fields of different ganglion cells overlap, so that

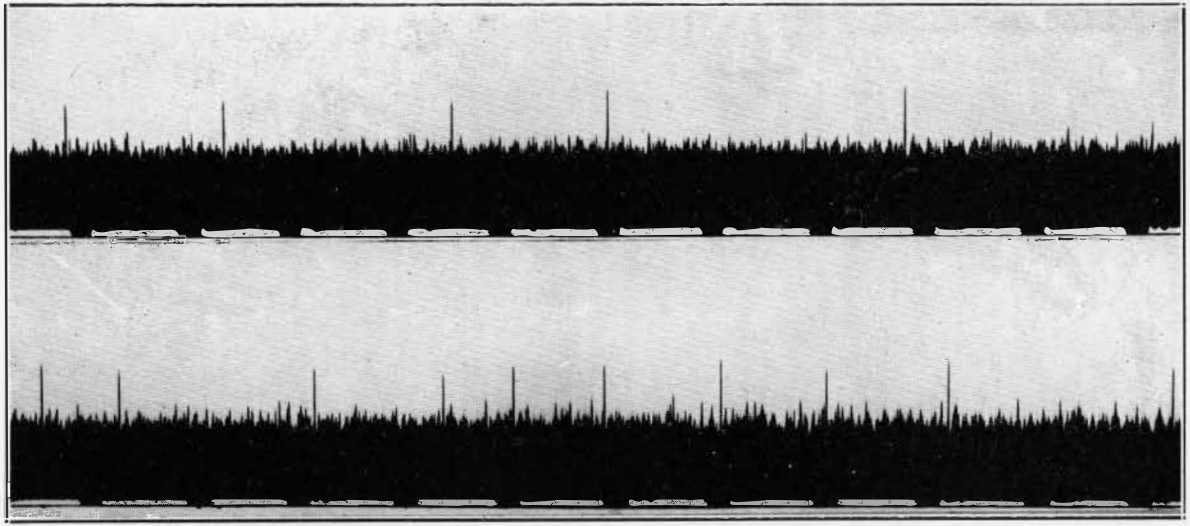


FIG. 19. Records of the maintained discharge of impulses in a single optic nerve fiber, showing effect of spatial summation. Top: response to illumination of most effective one of 9 subdivisions of an area of the retina (small square labelled 2.6 in Fig. 18). Bottom: response to illumination of entire area covered by the 9 subdivisions (labelled 4.3 in FIG. 18). Time marked in 1/5 sec. (Hartline (24)).

illumination of a given small area on the retina can excite several optic nerve fibers. This may be observed experimentally in bundles which have not been split by dissection, so that many optic nerve fibers remain active (23). Usually the activity in the various fibers can be distinguished (if there are not too many of them) by slight differences in their impulses, as observed with the aid of an oscilloscope. From such experiments it is possible to reconstruct the representation in the optic nerve of an illuminated point on the retina. A given element of retinal area lies within the central, most sensitive region of the receptive fields of certain retinal ganglion cells. The axons of these cells will be stimulated effectively by illumination of this element of area. For other cells this point lies in the less sensitive margins of their receptive fields; these cells will be activated less strongly by illumination of this particular element of retinal area. Illumination of a particular point on the retina therefore elicits a specific pattern of activity among the fibers of the optic nerve. The specific fibers involved, and the relative strengths of the discharges of nerve impulses they transmit, are characteristic of this particular point. Corresponding to other points are different patterns of activity; even two closely adjacent points do not produce quite the same distribution of activity, although they may excite many fibers in common. This may be observed directly, by watching on the oscilloscope the altered pattern of electrical activity resulting as a small spot of light is tested at different positions on the retina. For two points of the retinal image to be resolved, they need not necessarily be separated so widely that they activate entirely different groups of optic nerve fibers; it might suffice if two discrete maxima of activity are produced among the fibers involved. Nevertheless, one can hardly expect the resolution of detail to be as good as in the fovea, where each optic nerve fiber probably corresponds to only one receptor element.

The experiments reviewed in this lecture constitute the first steps in the unitary analysis of the mechanism of vision. They have shown that the visual sense cells initiate trains of nerve

impulses closely resembling the sensory discharges from other kinds of receptors. Evidence for the photochemical basis of the sensitivity to light of the visual receptor cell has been provided, but the processes intervening between the initial action of light and the final discharge of nerve impulses are not yet understood. The sensory information from receptor elements acts in turn upon higher neurons in the visual pathway. The early part of this process has been studied by recording the responses of the ganglion cells of the vertebrate retina. Their activity has been found to be governed by principles of nervous action well known from studies of the central nervous system. The study of these retinal neurons has emphasized the necessity for considering patterns of activity in the nervous system. Individual nerve cells never act independently; it is the integrated action of all the units of the visual system that gives rise to vision.

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