THE RESPONSE OF SINGLE OPTIC NERVE FIBERS OF THE VERTEBRATE EYE TO ILLUMINATION OF THE RETINA

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In a series of three papers Adrian and Matthews (1927, 1928) presented a study of the discharge of impulses in the optic nerve of the eel's eye, and so opened a new approach to problems of visual physiology. In those papers the simultaneous activity of large numbers of optic nerve fibers was recorded. The possibility of extending that work to an analysis of the activity in single optic nerve fibers was suggested by the subsequent investigation of Hartline and Graham (1932) on the optic nerve fibers of a primitive arthropod eye (Limulus). The present paper describes the discharge of impulses in single optic nerve fibers of the cold-blooded vertebrate eye, in response to illumination of the retina.

METHOD. The usual methods for obtaining action potentials from only one fiber in a nerve trunk have not succeeded when applied to the vertebrate optic nerve. It is therefore necessary to utilize the intra-ocular portion of the optic nerve fibers, by exposing the fundus of the eye and dissecting small bundles of fibers from the anterior (vitreous) surface of the retina, where they converge to the head of the optic nerve.

From a freshly pithed animal (in most of these experiments large bull-frogs (Rana catesbiana) were used) an eye is excised, pinned fundus down in a moist chamber, and its anterior half (cornea, lens, choroid body) removed. A wide V-shaped cut extending almost to the nerve head gives access to the fundus and permits the vitreous humor to be drained away. It is then possible to dissect free small bundles of nerve fibers for a length of 1 to 2 mm., and these may be further dissected until only one fiber remains active. A bundle is severed where it enters the nerve head and the cut end lifted up onto one of the electrode wicks; the second electrode is diffuse, touching the surface of the retina. The action potentials from such bundles of nerve fibers are amplified and recorded by means of an oscillograph. The preparation is mounted in a light-tight, electrically shielded box, in the hollow walls of which water at constant temperature (ca. 20°C.) is circulated.
Prepared in this manner the retinas of most cold blooded vertebrate eyes survive for 4–8 hours, as evidenced both by the normal type of retinal action potentials which can be obtained from them (cf. Chaffee, Bovie and Hampson, 1923) and by the normal responses and lack of spontaneous activity in nerve fiber bundles freshly dissected from the retina. Fine bundles themselves, after having been lifted away from the retina, rarely remain conducting for more than an hour or two, and usually fail to show action potentials in a much shorter time. Attempts to obtain single fibers are successful in only a very small percentage of trials.

Light from a concentrated tungsten filament lamp is focussed by a condensing lens 12 mm. in diameter upon an objective lens, which in turn forms an image (3 size) of the illuminated condensing lens upon the retina. A 45° prism close to the objective lens reflects the light downward onto the retina; it can be rotated so as to project the rays at approximately normal incidence onto that portion of the retina from which the nerve fibers in any particular bundle come. At the condensing lens can be placed a suitable diaphragm to limit the size and shape of the illuminated area; this diaphragm is carried on crossed micrometers controlling its position to within 0.01 mm., and its image is accurately focussed on the retina by micrometer movements carrying the preparation itself. The intensity of illumination upon the retina can be reduced by known amounts with Wratten Neutral Tint filters; the full intensity (no filters in the beam) is 2.10^4 meter candles.

Results. The discharge of impulses in any moderately large bundle of intraocular optic nerve fibers of the vertebrate eye is similar to that previously described for the whole optic nerve. Beginning several hundredths of a second after the light is turned on, there is a strong, brief outburst of impulses. Impulses continue to be discharged at a low rate as long as light continues to shine, and when it is turned off there is a renewed vigorous outburst which subsides gradually. Such responses were initially described by Adrian and Matthews (1927) in the eel's optic nerve and subsequently recorded by Granit (1933) from the mammalian optic nerve. It is not until the bundles have been dissected down until only one, or at most only a few, fibers remain active that a new and striking property of the vertebrate optic response is revealed. For such experiments show conclusively that not all of the optic nerve fibers give the same kind of response to light. This diversity of response among fibers from closely adjacent regions of the same retina is extreme and unmistakable; it does not depend upon local conditions of stimulation or adaptation, but appears to be an inherent property of the individual ganglion cells themselves.

Types of response. In figure 1 are records of the action potentials in single optic nerve fibers of the frog's retina. Figure 1A shows a response
in which the initial burst of impulses, at high frequency, is followed by a steady discharge at much lower frequency which lasts throughout the duration of illumination. When the light is turned off this discharge stops. Such a response is similar to that from a simple photoreceptor, observed in Limulus optic nerve fibers, even to the short pause following the initial burst. But while Limulus optic nerve fibers invariably show this type of response, in the frog’s retina it is obtained in less than 20 per cent of the fibers. The other fibers show strikingly different types of response. At least 50 per cent respond (fig. 1B) with a short burst of impulses at high frequency when the light is turned on, but show no im-

Fig. 1. Oscillographic records of the action potentials in three single intraocular optic nerve fibers of the frog’s eye, showing three characteristic response types.

A. Response to illumination of the retina consisting of an initial burst of impulses, followed by a maintained discharge lasting throughout illumination. There is no response to cessation of illumination in this fiber (the off response in this record is partly due to retinal potential, partly to another fiber which discharged several small impulses). See also figure 6.

B. Response only to onset and cessation of light. See also figure 2, figure 5A and C.

C. Response only to cessation of illumination. See also figure 5B, D and E.

In this and subsequent records, the time is marked in \( \frac{1}{2} \) second, and the signal marking the period of illumination fills the white line immediately above the time marker.

pulses as long as it continues to shine steadily; when the light is turned off there is another brief outburst of impulses. Such responses constitute the most prominent feature of the vertebrate optic response—bursts of impulses occurring only when the conditions of illumination on the retina are changed abruptly. In a third type of response, occurring in about 30 per cent of the fibers, no impulses appear at all during illumination, but there is a vigorous discharge of impulses when the light is turned off (fig. 1C). This discharge may last many seconds, and usually subsides gradually. It is undoubtedly responsible for most of the “off” response obtained from the whole optic nerve.

Most of the optic nerve fibers in the vertebrate eye give responses similar
to one or another of the above described types. These categories, however, are not absolutely rigid, and it would be a mistake to ignore the occasional fiber whose response is intermediate in character. Thus it is not infrequently found that a fiber whose response is of the first type has a maintained level of discharge of a low and irregular frequency, which tends to adapt out after several seconds. No clear-cut cases have been found in which a fiber giving an initial burst followed by a maintained discharge has shown an "off" response; the doubtful cases which have been recorded could have been due to a second fiber, as is the case in figure 1A (see fig. 6A for a clear-cut case, where there is no additional fiber giving an "off" effect). Fibers have been found, however, whose response lacks the initial burst; in these rare cases the discharge builds up slowly (in 2–3 sec.) to a steady level of ca. 20 to 30 per sec. When the light is turned off these fibers do show an "off" effect—a distinct increase in frequency for several tenths of a second before the discharge subsides. It is true that fibers which respond predominantly to a change in intensity with "on" and "off" bursts may occasionally show very irregularly scattered impulses or bursts of two or three impulses every few seconds during steady illumination. This, however, is quite different from the regular discharge of figure 1A, and may be regarded as an atypical, intermediate variety of response. Furthermore, fibers showing predominantly an "off" response are occasionally found in which a few scattered impulses "escape" during prolonged illumination.

From these observations it follows that the responses of the entire optic nerve are complex, containing different contributions from different fibers. An analysis of the optic response must therefore take up the properties of the different types of single fiber response separately.

Effect of intensity. Chief among the factors governing the response in any single fiber is the intensity of illumination with which the retina is stimulated. In figure 2 is shown a series of records of the responses to lights of different intensity of a single fiber of the "on-off" response type. With higher intensities of light the responses show shorter latent periods, higher maximum frequencies of discharge and greater numbers of impulses in both the "on" and the "off" bursts. This holds from threshold to intensities 4–5 logarithmic units above it. In figure 3 are plotted, on the left, the reciprocals of the latent periods and, on the right, the frequencies of the discharges (measured from the first six impulses) for both the "on" and the "off" bursts in this same fiber. In this fiber the threshold intensity was the same for both the "on" and the "off" bursts; frequently, however, one or the other of the bursts may have a somewhat lower threshold (usually within one logarithmic unit). It is to be noted that the curves rise abruptly from threshold—frequently the weakest response obtainable has a fairly large number of impulses, at a fairly high frequency.
While the threshold is sharp, it is not always reliable, and may fluctuate in spite of carefully controlled conditions.

The experiment of figure 2 and figure 3 shows the very considerable range over which intensity is effective in speeding up the discharge. This might be expected in view of the wide range which is covered by single visual sense cells in the Limulus eye (Hartline and Graham, 1932). This experiment also shows the characteristic effect of very high intensity in reducing the number of impulses and often the frequency of discharge in the bursts. This is especially pronounced for the "off" burst, which may be entirely missing at the highest intensities available.

Similar effects of intensity can be shown for the other types of response.
Fig. 3. The relation between intensity of stimulating light and response in a single optic nerve fiber of the frog's eye. Data from experiment of figure 2. On left the ordinates give reciprocal latent period (T_L, sec.): circles give values for "on" burst, dots for "off" burst. On right, ordinates give frequency (impulses per sec.) for the first six impulses of the bursts; circles give values for "on" burst, dots for "off" burst. Abscissae, in both graphs, give the logarithms (base 10) of the stimulating intensity. When no response appears, 1/T_L is assigned a value of zero; if fewer than 6 impulses are discharged, F_{1-6} is given a value of zero.

Fig. 4 A. The relation between the logarithm of intensity of retinal illumination (abscissae) and frequency of response (ordinates) in a single optic nerve fiber of the frog's eye. This fiber gave a response consisting of an initial burst followed by a discharge which was maintained throughout illumination. Dots and circles give, respectively, initial and maximum frequencies (three impulses) of initial burst; crosses give the frequency attained after four seconds of steady illumination.

Fig. 4 B. The relation between intensity and response of a single optic nerve fiber in the frog's eye. This fiber gave a response only upon cessation of illumination. Abscissae give the logarithms of the intensity of light. Ordinates (F_{1-6}, on the left) for the circles give the frequency (impulses per second) for the first six impulses; ordinates (N, on the right) for the dots give the total number of impulses in the burst.
In figure 4A are plotted the frequencies of various parts of the discharge in a fiber giving an initial burst followed by a maintained discharge. The initial frequency (first three impulses) and maximum frequency (usually between the 5th to 8th impulse) of the initial burst are given, together with the final level of frequency attained after four seconds of steady illumination. This graph may be compared with a similar plot for the *Limulus* single optic nerve fiber (Hartline and Graham, 1932, fig. 6). At low intensities, near threshold, the maintained discharge usually adapts out completely after a second or two, and often only the initial burst can be obtained.

The degree of activity in a fiber giving only an “off” response is also dependent upon the intensity of the light. In figure 4B are plotted the initial frequencies of the discharge from such a fiber, in response to cessation of lights of different intensities. The sharp threshold, and the diminished values at high intensities are similar to the corresponding plot of the “off” burst of figure 3. This particular fiber gave a rather short, sharply defined burst not unlike the “off” response in a typical “on-off” fiber. This enabled a reliable count to be made of the total numbers of impulses in the bursts, also plotted in figure 4B. Usually, however, as has been said, the discharge in a fiber giving only an “off” response is prolonged, and dies down very gradually. (Compare fig. 1B with C; fig. 5A and C with B, D and E.) The higher the intensity the longer does the discharge last; at very high intensities the initial part of it may be reduced to a few impulses, but after several seconds it is gradually resumed, and may persist for many minutes at a frequency which may be as high as twenty or thirty impulses per second. Several instances have been observed where such a discharge broke up into rhythmic bursts, coming at about 3 to 5 per second.

**Change in intensity.** The amount of change in intensity also affects the magnitude of the responses. Fibers which discharge a brief burst of impulses in response to the onset and cessation of illumination also respond to a sudden increase or decrease in its intensity (fig. 5A); the bursts, however, have fewer impulses at a lower frequency. Likewise the “off” fibers will respond, though less strongly, if the illumination is partially reduced (fig. 5B) but not if it is increased in intensity. The frequency of the maintained discharge in those fibers which show such a response is of course determined only by the level of the steady illumination—an increase or decrease in intensity results in a corresponding rise or fall in frequency (fig. 7C).

**Light and dark adaptation.** A given intensity of light is effectively weaker in the light adapted retina than after dark adaptation. As dark adaptation proceeds the response to a given intensity increases, and correspondingly the threshold falls, rapidly at first and then more gradually.
After one half hour in the dark a fiber may respond to light 1/100 to 1/1000 the intensity of that necessary to elicit a response in the light adapted condition. The essential character of the response in any given fiber, however, is unchanged by adaptation. Reliable quantitative measure-ments of the effect of adaptation in these experiments are difficult to obtain, owing to the comparatively short time fibers stay alive in a dissected bundle.

Duration of exposure. The strength of an "off" response at a given intensity depends on the length of time the preceding light has been al-

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**Fig. 5.** Records of the impulse discharge in single optic nerve fibers of vertebrate eyes. Record B is from an alligator, the rest are from frogs. Recording as in figure 1.

A. Response to a partial reduction and to an increase in intensity of an "on-off" fiber. Left to right: Onset of light (log I = -2.0); intensity reduced by 0.5 log unit; intensity increased to original value; light turned off.

B. Response to partial reduction in intensity in a fiber giving only "off" responses. Left to right: light of an intensity log I = -2.0 reduced in intensity by 0.7 log unit; (a length of record equivalent to 1/2 sec., showing a gradually decreasing discharge, has been removed) light increased to original intensity; (a length of record equivalent to 1 sec., showing no impulses, has been removed) light turned off; (a length of record equivalent to 1 sec., showing a steadily decreasing discharge, has been removed) light turned on again.

C. (Time scale same as in the other records.) Effect of exposure in producing an "off" burst in an "on-off" fiber. Left to right: exposures, to a constant intensity, of 0.18 sec., 0.70 sec., 3.0 sec. Exposures made successively within about 10 seconds of each other, hence the "on" bursts in last two records are somewhat weaker than in first record, taken in the completely dark adapted condition.

D. Same as C for a fiber giving only an "off" response. Left to right: exposure to a constant intensity of 0.20 sec. and of 2.2 sec.

E. Inhibition of "off" discharge by re-illumination. (See also B of this fig.). After an interruption of 0.23 sec. light is turned on again (middle section of record); full "off" response shown in last section of record.
allowed to shine. It is entirely absent following short flashes, and in general is stronger the longer the exposure. This is true for the fibers giving both "on" and "off" bursts (fig. 5C) as well as for fibers giving only "off" responses (fig. 5D). Similarly the "on" burst will be absent or weak unless there has been a sufficiently long period of darkness preceding (fig. 7B). The exact time requirements for the development of the "on" and "off" bursts vary widely with different fibers.

**Inhibition of the "off" response.** The presence, in the vertebrate eye, of a fair percentage of fibers responding only when the light is turned off or reduced in intensity is one of the somewhat surprising findings of the present study. Although no impulses appear in such fibers during illumination, it is to be emphasized that the "off" discharge depends upon the preceding period of illumination for its excitation. The effect of this excitation does not appear until after the stimulating agent has been removed. Indeed, if the retina be re-illuminated before an "off" response has subsided, the discharge is abruptly suppressed. This may be seen in figure 5E, by comparing the effect of the brief interruption of the illumination with the fully developed "off" response following permanent cessation of the light. A very brief interruption (shorter than the latent period of the "off" response) will still give rise to a burst of impulses, but one which is very short and with considerably reduced impulse frequency. The prolonged "off" discharge following intense and prolonged illumination can always be stopped by re-illumination, even at considerably lower intensity. Following such a period of low illumination the discharge re-appears, augmented by the "off" response caused by cessation of the weak light.

This inhibitory action of light on the "off" discharge is one of the most striking features of the vertebrate optic response. Most of its effects which have been noted here have already been described in responses from the whole optic nerve (Granit and Therman, 1935; Granit and Riddell, 1934). The present results clarify the analysis considerably, by showing the roles played by different fibers. Thus the latency of the suppression of the "off" discharge is usually very short shorter than the latency of the "on" bursts in other fibers, especially under the conditions of light adaptation which necessarily exist. Hence in bundles containing many active fibers a brief pause occurs, shortly following re-illumination, during which no impulses are discharged (fig. 7B). This interval between the time when the activity in the "off" response fibers has been suppressed and the moment of appearance of the "on" bursts in other fibers probably corresponds to the "A" wave of the retinal action potential. As shown by Granit and Therman (1935), the principal effect of the "A" wave is to remove what "off" effect may be present; it is large when there is still a strong discharge in the "off" response fibers. When the discharge has subsided in most of these fibers, after dark adaptation, and the "on"
bursts in other fibers are stronger and have a shorter latency, the "A" wave is correspondingly small.

Stability of response types. a. Conditions of stimulation. It is to be seen from the preceding sections that the various types of response which are obtained in different fibers are characteristic of the particular fibers in question, rather than being due to the conditions of stimulation. Thus fibers giving "on" and "off" bursts, or only "off" responses do so over the entire range of intensities to which they respond; and fibers in which a discharge is maintained during steady illumination show this response for all intensities except near threshold. Likewise during light and dark adaptation of the eye, the type of response in any given fiber does not change. Frogs kept in bright sunlight for as long as 4-6 hours show no essential differences in the types of responses from those which have been kept in complete darkness for 48 hours, have had their eyes removed and prepared in red light, and the nerve bundles rapidly dissected in the weakest possible white light.

b. External factors. In order to test the possible influence of some of the more obvious external factors which might affect the retina, the following experiments were done. While not extensive, they do indicate a considerable stability in the essential features of the various response types. 

Asphyxia: if hydrogen is passed through the moist chamber, responses quickly become feeble and soon fail; they return to their former strength if oxygen is promptly readmitted. But at no time do they change their essential character during asphyxia. pH and CO₂: changing the pH of the Ringer's solution between 6.8 and 8.5 (phosphate buffers) with which the retina was then bathed for a few minutes produced no very apparent change in the responses, in one experiment. Two per cent CO₂ mixed with the air passed into the moist chamber causes reversible failure, with no change in the character of the responses. Ion unbalance: bathing the retina for a few minutes with Ringer's solution containing no calcium brings about a great increase in spontaneous activity, and tends to prolong the bursts of both the "on-off" and "off" types, with possibly some tendency to show "escape" of scattered impulses during illumination. Ringer's solution containing no potassium, on the other hand, abolishes even that spontaneous activity which may be present normally, and reduces the number of impulses in the bursts caused by change in illumination. In fibers which normally show a maintained discharge the response is not abolished, although its frequency may be reduced. These changes with unbalanced Ringer's solution are all reversible. Temperature: between 18° and 24°C. there is a marked speeding up of the responses with higher temperature, but there is no essential change in their character. Season: over a period of three years these experiments have shown no differences that could be correlated with the
season of the year, or whether the animals were freshly caught or had been kept in the laboratory.

Thus external agents which definitely affect the degree of response do not, however, change its essential character. That seems to be a fixed attribute of each particular ganglion cell.

**Responses in other vertebrates.** Responses in optic nerve fibers have been recorded in a variety of cold blooded vertebrates other than the frog. These experiments include one shark, one *Necturus*, a number of turtles and alligators, one iguana and several varieties of snakes. While not extensive, they show unmistakably the same general result that is found in the experiments on frogs. In the eyes of all these animals there are fibers which maintain a discharge as long as the retina is illuminated (or at least for the first several minutes), other fibers which give bursts of impulses only in response to changing the intensity of light, and still others which respond only when the illumination is reduced. Minor differences have, however, been found, and a more exhaustive comparative study might even reveal significant variation in optic function among different vertebrates. Thus in the experiment on *Necturus* the maintained discharge disappeared completely after a half minute exposure to light, and the "off" responses were feeble and required at least ten or more seconds' exposure before they could be elicited. And in both the turtle and alligator eyes fibers are not infrequently found giving only a brief burst when light is turned on, with neither maintained discharge nor "off" response. On the other hand, where one might expect to find striking differences, as in the pure cone retina of the snake, neither the actual types of response nor the relative frequency with which they were obtained differed notably from those in the mixed, though predominantly rod retina of the frog. (Only four satisfactory experiments have been done on the snake eye, since it is a difficult preparation.)

**Spatial effects.** No description of the optic responses in single fibers would be complete without a description of the region of the retina which must be illuminated in order to obtain a response in any given fiber. This region will be termed the receptive field of the fiber. The location of the receptive field of a given fiber is fixed; its extent, however, depends upon the intensity and size of the spot of light used to explore it, and upon the condition of adaptation; these factors must therefore be specified in describing it. For moderate intensities (less than ca. 4 logarithmic units above threshold) and small spots (of the order of 0.1 mm.) the receptive fields of most of the fibers of the frog's retina are roughly circular, with a diameter of the order of 1 mm. in the dark adapted condition. Even at threshold a small spot of light 0.05 mm. in diameter will usually elicit a response in most fibers anywhere within an area of ca. 0.5 mm. diameter. At higher intensities the size of this region from which a response can be
obtained is larger, but the strongest response is always obtained from the central portion of the receptive field; from the margins the response is usually of the threshold type (fig. 6). Thus the results of illumination of different points within a restricted region of the retina converge upon a given ganglion cell, and cause responses in its axone. This convergence extends over greater distances the stronger the stimulus; and for a given intensity the effects are strongest in the center of the region of convergence. Of particular importance to the present discussion is that, no matter what part of the receptive field is stimulated, the response in any given fiber is always essentially of the same type. This holds true for all types of response, and applies to stimulation anywhere within the receptive field. A few apparent exceptions have been observed, in which the type of response was different for different positions on the retina of the stimulating spot of light. In those cases where opportunity permitted a closer investigation, however, they proved to be either anomalous effects near threshold, or else due to two active fibers whose action potentials were so nearly similar as to be confused.\footnote{Such confusion does not arise very often, and when it does there is usually adequate opportunity to recognize the impulses due to separate fibers when the bundle begins to die, since it is very unlikely that different fibers will fail to conduct at the same time and show the same changes in the form and magnitude of their action potentials.} If true exceptions do exist, they must be quite rare; nevertheless they would be of considerable significance in explaining the diversity of the response types.

No correlation has been noted between the type of response given by a fiber and the location in the retina of its receptive field; all response types
can be obtained from any part of the retina. (Whether this holds true for the foveal region in animals possessing a well-defined rod-free area needs to be determined.) Indeed, the receptive fields of different fibers picked up in the same bundle frequently overlap considerably, and in fortunate preparations, where impulses in different fibers can be clearly distinguished by differences in the form and magnitude of their action potentials, it is easy to show that fibers with different types of response

![Fig. 7. Records of the discharge of impulses in bundles of optic nerve fibers of vertebrate eyes, each showing different types of responses in different fibers from the same region of the retina.](image)

A. Bundle from turtle's eye, showing one fiber giving "on" and "off" bursts (large impulses); another discharging impulses throughout whole period of illumination (small impulses); and a third giving only a brief "off" response (medium sized impulses).

B. Bundle from frog's eye, showing two active fibers, one giving typical "on" and "off" bursts (large impulses), the other responding only to turning light off. Re-illumination after 0.36 sec. (middle part of record) stopped the discharge in fiber giving only the "off" response (compare with last part of record, where light was left off) and produced a very weak "on" response in the "on-off" fiber.

C. Bundle from frog's eye, showing a fiber (small impulses) which maintained its discharge at a low frequency during period of illumination at beginning of record. Intensity doubled, this fiber gave an initial burst and then maintained its discharge at a higher level of frequency. Intensity reduced to its former value; frequency in this fiber dropped, and another fiber responded with a vigorous "off" response, (large, thin impulses). A third fiber (medium sized, thin impulses) gave a short burst in response to the increase, and very few impulses (difficult to distinguish) in response to the decrease.

are usually present and are stimulated simultaneously by a small spot of light (fig. 7). Such observations constitute good evidence for the distinctness of the response types, for they are obtained under identical conditions of adaptation, stimulation, and external environment.

**Discussion.** From this experimental study it is apparent that each individual ganglion cell has a relatively fixed character of response, which, with few exceptions, falls under one of three distinct types. Concerning
the explanation of this rather unexpected result one can only speculate. The retina, of course, does not possess a homogeneous population of end-organs, and it is possible that the different types of response originate in different types of visual sense cells, merely being relayed through the ganglion cells unaltered. Thus the rods and cones might give rise to responses of different types. Ignoring for the moment the presence of all three types of response in the pure cone retina of the snake, it is still difficult to fit three response types into a duplicity theory, and evidence is still lacking that would associate any of the response types with either rod or cone function. But different forms of both rods and cones are present in most cold-blooded vertebrate retinas, and different sense cells show adaptation of their responses in different degrees. It is not unreasonable to assume that certain of either the rods or cones, or both, might adapt completely following their initial discharge of impulses. Even pure "off" responses might be supposed to originate in certain cells excited by a shift in their equilibrium in the sense opposite to that which usually gives rise to the discharge of impulses.

The diversity of response might, on the other hand, originate in the layers of the retina between the rod and cone layer and the ganglion cells. Thus a given ganglion cell may be subject to diverse and rival influences, and its response determined by the relative amounts of each. This, in turn, may be fixed in large measure by the anatomical connections between the ganglion cell and its underlying neurones. This study in fact has shown clearly that the excitation produced by light may be subject to modification by an influence which may justifiably be termed inhibitory. Thus the relative amounts, and rates of rise and fall of excitatory and inhibitory influences upon a ganglion cell might determine its response. The "off" effect may then be due to a post-inhibitory release of the effects of an excitation which are all the greater for having been suppressed during the actual period of illumination. Granit and his co-workers have urged the use of these concepts in the interpretation of optic response.

Still another explanation to be considered is the possibility that functional differences may exist among the ganglion cells. While subject to essentially the same influences from the underlying retinal layers, different ganglion cells may respond differently to shifts in their equilibrium. The further consideration of these and other possibilities must wait upon the results of further experiments.

**SUMMARY**

1. Action potentials in single optic nerve fibers of cold-blooded vertebrate eyes may be obtained from small intraocular bundles dissected off the anterior surface of the retina of excised, opened bulbs.

2. Responses in different single fibers from the same retina show differ-
ent types of response. In about 20 per cent of the fibers response to illumination of the retina begins with a burst of impulses at high frequency, followed by a steady discharge at lower frequency which is maintained throughout illumination, and stops when the light is turned off. About 50 per cent of the fibers show only a burst of impulses in response to the onset of illumination, and another in response to its cessation; no impulses are discharged during steady illumination of the retina. The third type of response, obtained from about 30 per cent of the fibers, shows no discharge either at the onset of illumination, or throughout its duration, but gives a vigorous and prolonged discharge when the light is turned off.

3. In general the higher the intensity of retinal illumination the shorter is the latent period of the response, the higher its frequency of discharge, and the greater the number of impulses in a burst.

4. Fibers which give a response to the onset and cessation of light also respond, though less strongly, to an increase or a reduction in its intensity. Fibers giving only an “off” response respond, though less strongly, to a reduction in intensity; they give no response to an increase.

5. As dark adaptation of the eye progresses, the discharge which can be obtained from any fiber in response to a given intensity increases; the threshold of response correspondingly falls, rapidly at first and then more gradually, for half an hour or more.

6. “Off” responses are weak or absent following short periods of illumination; similarly “on” responses require a sufficiently long preceding period of darkness for their full development.

7. The discharge in fibers giving only an “off” response is promptly suppressed by re-illumination of the retina.

8. The type of response in any given fiber does not depend upon conditions of stimulation or adaptation of the eye. Even certain external agents (asphyxia, CO₂, ion unbalance, temperature), while affecting the responses do not alter their essential character.

9. Experiments on fish, amphibian and reptilian eyes give essentially the same results as regards the types of response found.

10. Responses can be obtained in a given optic nerve fiber only upon illumination of a certain restricted region of the retina, termed the receptive field of the fiber.

11. The location on the retina of the receptive field of a fiber is fixed. Its extent depends upon the size and intensity of the spot of light used to explore it, and upon the state of adaptation of the eye.

12. With possible rare exceptions the type of response in any fiber does not depend upon the portion of its receptive field which is illuminated.

13. The type of response in a fiber is not correlated with the location of its receptive field in the retina.

14. The question is discussed as to whether the diversity in types of
response is due to different types of sensory cells, whether it arises in the intermediate layers of the retina, or whether it is the result of functional differences among the ganglion cells.

REFERENCES

J. Physiol. 64: 279, 1927.
J. Physiol. 65: 273, 1928.


Granit, R. J. Physiol. 77: 207, 1933.
