



TWO TYPES OF RETINÆ AND THEIR ELECTRICAL
RESPONSES TO INTERMITTENT STIMULI
IN LIGHT AND DARK ADAPTATION.

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In his valuable paper on the retinal action currents of various types of eyes Piper [1911] showed that there were two types of reactions to intermittent stimuli: either (i) the first visible reaction to the individual stimuli was a positive wave, as *e.g.* in the cat, or (ii) it was a negative wave temporarily interrupting the off-effect elicited during the dark intervals, as *e.g.* in the pigeon. These differences refer to the wavelets, superimposed upon the summed response of the individual flashes, set up by intermittent stimuli at a rate just below the fusion frequency. In both cases the summed response begins in the ordinary way with a negative *a*-wave followed by a positive *b*-wave, as may be seen in several of the records published below. Creed and Granit [1933] found that in the first type of eye (cat) the latent period of the positive flickering wavelets was lengthened as compared with the initial *b*-wave, and held this to be due to activation of the negative component P III which for a moment counteracted the positive component P II without being able to elicit a definite negative wave. The differences between the two types of eyes would thus be quantitative rather than qualitative.

In this paper it will be shown that these two types of reactions to intermittent stimuli may serve to distinguish two types of retinæ which in several important aspects differ from one another. This being the case new terms seem to be fully justified, and below the term E-retina will be used to denote an eye in which intermittent stimuli cause positive wavelets, and the term I-retina for an eye in which the intermittent flashes of light cause negative "notches" in the (positive) off-effects, elicited by the dark intervals. The terms were suggested by the recent work by Granit and Therman [1935], who showed that the negative

“notch” in the response of the I-retina coincided with inhibition of the discharge in the optic nerve, whereas rapid positive deflections always were found to coincide with excitation in the nerve (cf. also Granit [1933], Creed and Granit [1933], for the cat's E-retina). Thus, to put it somewhat schematically in a preliminary way, the E-retina flickers with volleys of excitation, the I-retina with volleys of inhibition interrupting the “rebound” of impulses at “off”.

Below, these preliminary definitions of E- and I-retinæ will be extended, particularly with reference to state of adaptation. So far flicker and state of adaptation have been interrelated only with the frog's retinal action potential [Granit and Riddell, 1934]. Below, pigeons, owls, cats, and rabbits will be used, the aim of this particular selection of animals being to confront the concepts behind the duplicity theory with those gradually developing from a study of the electrical reactions in retina and nerve.

TECHNIQUE.

It is hardly necessary to describe the technique in detail, as both permanent magnet string galvanometer, amplifier, camera, lamp, and flickering fan in the beam of light were directly taken over from the work of Granit and Riddell [1934]. The ground-glass screen, used by the latter authors, was permanently removed and the lamp was allowed to shine directly on the animal's eye. If not otherwise stated, the intensity of the light, measured with a Lummer-Brodhun photometer at the distance used, was about 620 metre-candles at the animal's eye. Tscherning neutral tint glasses were used to reduce the intensity of the stimulus in some experiments separately referred to below.

The general procedure of the experiment was as follows: after the electrodes had been fitted on, the animal was given half an hour for dark adaptation inside the blackened box. Then some records of flicker in the dark-adapted state were taken, after which followed 10 min. of adaptation to the standard stimulus. As soon as the off-effect of the period of light adaptation had disappeared, the eye was ready for a record in the light-adapted state.

Allowing intervals of half an hour for dark adaptation this general procedure was often several times repeated with the same animal.

The two 90° sectors interrupting the beam of light were put into rotation by means of a cord, quickly drawn over a pulley, and the fan was then left to slow down at a rate determined by its own frictional forces. This means that the frequency of the intermittent stimuli always

changed from fast to slow, and as the fan was running on ball-bearings the change took place fairly evenly.

Successful experiments were made with 21 animals: 9 pigeons, 2 owls (*Syrnium aluco*), 6 cats, and 4 rabbits. The pigeons and owls were anæsthetized with "avertin", their necks fixed into metal collars, and their beaks tied down to a protuberance on the collar. "Avertin" was given (*per rectum*) before every period of dark adaptation. The pigeons were killed after the experiment, as it had been necessary to cut away their lids and nictitating membranes (wounds anæsthetized with cocaine), but the owls were experimented upon several times at intervals of a few days. Their lids were kept apart by a specially designed clamp and their corneæ were cocainized for the corneal electrode. A small likewise cocainized incision was made in the skin above the eye for the other electrode. Cats and rabbits were treated in the same fashion when "dial" or "somniafer" was given. In addition a drop of atropine was given to immobilize the pupil. The iris of birds is striated and does not react to atropine, but the pupil reflex is very rapid and probably over when fusion is reached. Besides, the change in the fusion frequency with state of adaptation runs counter to the effect to be expected from a change in the size of the pupil.

The cats were decerebrated in the usual way and left to become dark adapted with the electrodes inserted. With one cat "dial" was tried. Three rabbits received "dial" and one "somniafer". Though with a moderate dose of "dial" the retinal response is reasonably good, yet the animals, especially the rabbits, were rather restless under it, and the base line was not altogether satisfactory.

RESULTS.

The frog's eye will be used as a standard of comparison to which the results obtained with the other eyes will be referred on the basis of a type of experiment in sequence with the work of Granit and Riddell [1934]. Their procedure was to throw in short flashes of light at various points along the off-effect, but here the flashes have been replaced by a continuous stimulus. This in practice amounts to systematic lengthening of a "gap" of darkness in an otherwise continuously illuminated eye. The latter method has been used by Piper [1911] with dark-adapted eyes, but in this work light adaptation has been used, since in the photopic state it is easier to see whether an eye belongs to the E- or I-type.

The result of this experiment with the frog's eye is shown as the series of curves marked A in Fig. 1. The first effect of the reappearing stimulus is a negative "notch" varying characteristically in size with its

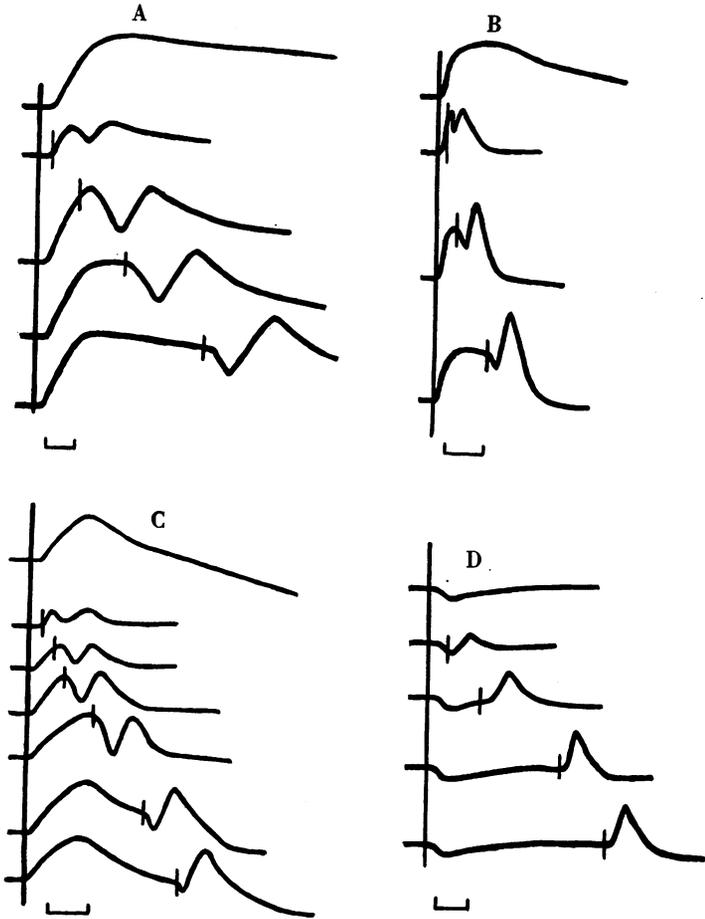


Fig. 1. In each series of curves the long vertical line marks end of stimulation with standard light; the short vertical on the individual curves marks reappearance of stimulus; the interval between them duration of gap of darkness. The uppermost curve in every series shows the uninterrupted off-effect. Time below each series 1/10th second. Series A obtained with a frog, B with a pigeon, C with an owl, and D with a cat.

locus on the off-effect. This is typical of the I-retina, and the effect was shown by Granit and Riddell [1934] to depend upon reactivation of the negative inhibitory component P III. The negative "notch" is an

a-wave, the positive peak following it is a *b*-wave [Granit and Riddell, 1934].

In dark adaptation these negative waves are much smaller and slower, showing that the inhibitory component is smaller and slower in this state of adaptation, as proved in detail by Granit and Riddell [1934].

Now flicker may be regarded as a series of "gaps" of darkness in an otherwise continuous stimulus. In the frog's eye then each gap of darkness elicits an off-effect, each phase of light a negative "notch" of the inhibitory component P III. The fusion frequency during light adaptation is about 20 flashes per second. It decreases during dark adaptation to about 6-7 flashes per second, or, say, by some 70 p.c. In the slowly flickering dark-adapted eye both troughs and crests of the undulations are reduced in size and rate of rise. After some minutes of light adaptation a most striking change takes place: brisk waves with deep troughs and sharp crests appear, and this change can be measured by recording the fusion frequency.

Granit and Riddell [1934] showed that the main factor behind the increase in the fusion frequency after light adaptation was an increase in the inhibitory component P III, responsible for the negative phase and the off-effect, but the positive peaks are also sharper in the photopic eye and this may indicate a small change in the excitatory component P II. With a continuous stimulus the increase in the inhibitory component after light adaptation is easily judged by the size and rate of rise of the off-effect, or by an experiment of the type described above (Fig. 1).

The pigeon's retina.

The frog's retina is a rod retina with a great number of cones. The pigeon has a retina dominated by cones. A large central area is probably almost rod-free, and so are the two foveæ, lateralis and nasalis. Towards the peripheral parts rods appear, though never in great numbers. Small amounts of visual purple have been extracted from the pigeon's retina by Hess [1912]. Both rods and cones have dendritic connections with the bipolars. There is little "inward convergence"; even as far towards the periphery as 6.8 mm. from area centralis there are only 15 receptors pro ganglion cell [Chiewitz, 1889]. Highly developed inward convergence on the whole seems to run parallel with the appearance of rods ending in knobs instead of in dendrites [Ramón y Cajal, 1933].

As an experimental animal for electrophysiological work the pigeon belongs to the more difficult ones. If the bird is deeply anæsthetized its

retinal response is easy to record, but then the secondary rise or *c*-wave is flattened out (cf. Granit [1933] for the same result with cats), and the other phases also have diminished and slowed down. Most birds, therefore, were lightly anaesthetized with the result that several records looked like A (Fig. 2), which obviously is distorted by eye movements. These do not interfere with the determination of the fusion frequency if fusion happens to fall into a quiet phase, but it may be difficult to be certain about other changes due to adaptation unless they are very large. The two other records of Fig. 2 B and C are from a lightly anaesthetized fairly quiet bird. The upper curve (B) is taken after dark adaptation, the lower record shows the result after 10 min. of adaptation to the standard light. The fusion frequency in the scotopic response is 38.5, in the photopic one 45.5.

Altogether 110 records of flicker were taken. In none of these did the fusion frequency of the dark-adapted eye sink below the value obtained after light adaptation, though in some cases the values were identical. As a rule the fusion frequency fell during dark adaptation. The values averaged out at 45 flashes per second in light adaptation and 40 flashes per second in dark adaptation. Calculating the drop in the fusion frequency of the scotopic eye as above for the frog's eye the figure obtained is 11 p.c. With the best eyes the maximal fusion frequency went up to 55 (light adaptation), indicating that anaesthesia was responsible for the lower average of 45.

As to other changes due to light adaptation there seems to be a small increase in the size and rate of rise of the off-effect and likewise a favourable effect on the secondary rise. The *a*- and *b*-waves do not seem to alter. The pigeon's eye develops a maximal potential of about 0.2 mV. for the *b*-wave as compared with up to 1.0 mV. for the frog's eye. The increase in the *c*-wave following light adaptation was noted by Kohlrausch [1918], who pointed out that in this respect the pigeon's retina differs from retinae of nocturnal animals in which the *c*-wave diminishes after light adaptation. Kohlrausch states that the secondary rise completely disappears during dark adaptation of the pigeon's eye, whereas in my experiments it has always been present and only slightly diminished in the dark-adapted state. His results may have been due to more efficient light adaptation, but it is not improbable that the small *c*-waves of the dark-adapted eyes had to do with his use of curare and artificial breathing.

The most significant result of these experiments is not that the pigeon's retinal responses change a little with changes in the state of

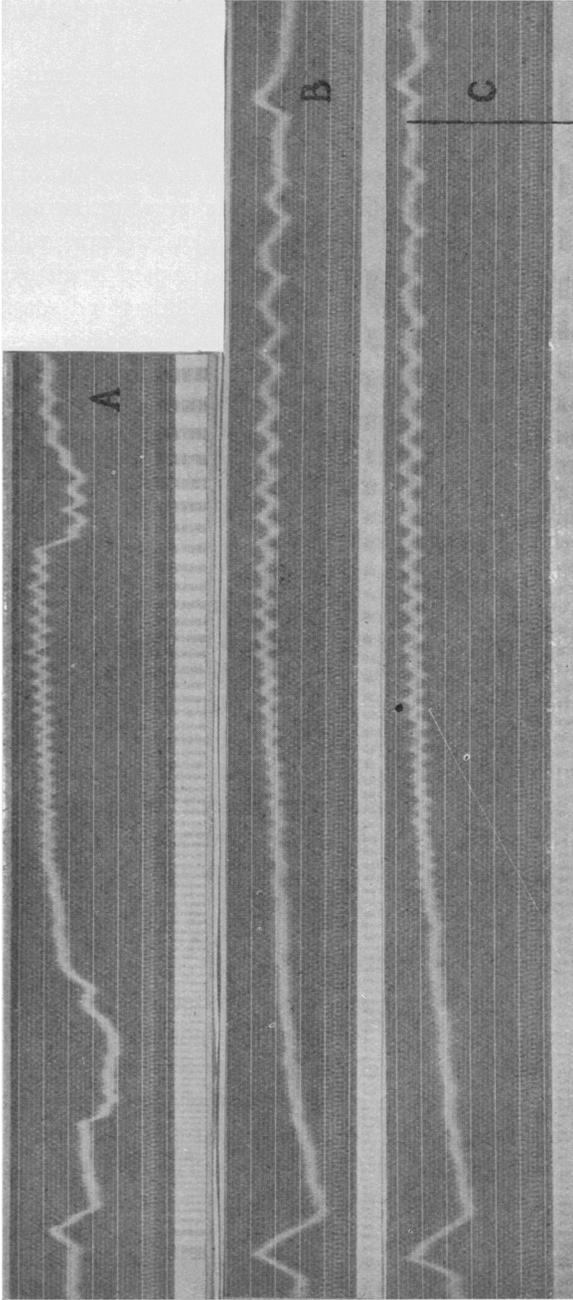


Fig. 2. A, flicker in the retina of lightly anesthetized restless pigeon. B and C from another pigeon; B, dark adaptation; C, light adaptation. Fairly high sensitivity; 1 mV. corresponds to 54 mm. and b-waves of B and C equal 0.16 mV. Below, retinal response tuning fork record marking intervals of 10σ , and stimuli, directly photographed. Vertical line on C shows onset of last intermittent flash. Note negative effect on retinal response. Explanation in text.

adaptation, but that the retina of this bird is fairly stable and relatively independent of state of adaptation.

The series of curves, marked B in Fig. 1, shows the result of the experiment with "gaps" of darkness. Obviously the pigeon has an I-retina in which the size of the negative "notch" varies less than in the frog's eye with its locus on the off-effect. Fig. 2 also shows that at slower rates of flicker the first effect of the flashes is a negative swing of the galvanometer. The same type of flicker may be seen in curves, published by Granit and Riddell [1934], from the light-adapted frog's eye. The difference between the two I-retinæ with regard to flicker and adaptation is that the retina of the frog must be light adapted in order to react as the pigeon's retina, independently of state of adaptation, does. Only in the photopic frog's eye is there a large off-effect, a rapid negative "notch" and a high fusion frequency. Since in the pigeon's eye the *b*-wave remains constant despite changes in state of adaptation, the small increase in the fusion frequency of the photopic state must depend on the change in the off-effect which, though smaller in degree, is in the same direction as the corresponding change in the frog's eye.

In the frog's eye the secondary rise disappears after light adaptation, whereas in the pigeon's eye it persists and even increases a little so that the contour of the photopic responses is rather different in the two types of eyes. But as the secondary rise—largely if not altogether due to the slow positive component P I [Granit, 1933]—cannot be shown to have anything to do with the frequency of the impulses in the optic nerve [Granit and Therman, 1935], nor with flicker [Piper, 1911; Creed and Granit, 1933], differences in the secondary rise would seem to be of less importance than changes in the fusion frequency which are carried upwards by the optic nerve.

The owl's retina.

The retina of this owl (*Syrnium aluco*) was studied by Schultze [1866] in the classical work that led to the important deduction that rods are specific receptors for twilight vision. But Schultze's statement that cones are scarce in the retina of *Syrnium* was soon contradicted by Krause [1894] who came to the conclusion that the owl has as many cones per sq. mm. as the buzzard (*Falco buteo*). The difficulty seems to be that numerous slender rods cover the cones, which also have paler colour globules than those found in many other birds, so that this otherwise very useful criterion fails to give the necessary aid in the search for cones. After consultation of a number of standard monographs on the

retina [Pütter, 1912; Hess, 1912; Franz, 1904, 1934; Ramón y Cajal, 1933; Rochon-Duvigneaud, 1934] one cannot doubt but that the owl's retina contains a considerable number of cones. Hess counts $2\frac{1}{2}$ millions. On the other hand, it is obvious that it has innumerable rods compared with retinæ of diurnal birds. The dark-adapted owl's retina is coloured deep red with visual purple.

The owl has only a fovea lateralis for binocular vision, as its eyes are directed forwards. There are rods in the fovea too, and Franz [1934] is not even certain as to whether the cones increase in number towards the fovea as in most other animals including diurnal birds. In the owl's retina the 1 : 1 relation between receptors and ganglion cells is nowhere reached. Even in the fovea there are 7·2 receptors for 1·4 ganglion cell [Franz, 1934]. Towards the periphery convergence increases.

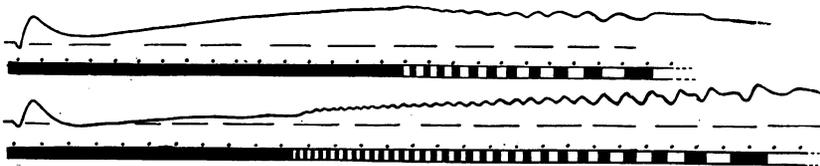


Fig. 3. Owl's retina responding to intermittent stimulation. Upper curve: dark adaptation; lower curve: light adaptation. Time in 1/10th sec. Stimuli in this figure, and in those to follow, black and separated from each other from the beginning of flicker onwards. Base line of galvanometer broken line.

The rudimentary eye muscles do not seem to be able to move the large telescopic eye, so that this bird is an ideal preparation for electrophysiological work. The owl has excellent vision in daylight, as no one will doubt who for some time has kept one in captivity. Their nocturnal habits are facilitated by the visual purple mechanism but probably more dependent upon the well-developed acoustic apparatus.

How well the owl's eye reacts after light adaptation may be seen in Fig. 3, in which the upper response is taken after dark adaptation, the lower one after light adaptation. The *b*-waves in the dark-adapted state fall around values between 0·5–0·6 mV., in this case it is 0·55 mV. After light adaptation it falls only to 0·47 mV. The secondary rise is slightly reduced and slowed down in the photopic eye. As in the frog's eye, the most striking change after light adaptation is an increase in the size and rate of rise of the off-effect. This is best seen with a continuous stimulus but also visible in the records of Fig. 3. A well dark-adapted owl's eye may show merely a retardation of the fall at "off" after an exposure of a few seconds, reminiscent of the type of off-effect seen in cats, but after

light adaptation there is always a well-marked rise at cessation of illumination.

From the change in the off-effect after light adaptation it is possible to predict that the fusion frequency will be higher in the photopic eye, as shown by the curves of Fig. 3. In the upper response there is fusion at 17 flashes per second, in the lower one at 33. When all 34 observations are averaged the difference is smaller: the fusion frequency is 22 in the scotopic eye and 34 in the photopic state. Thus the average drop after dark adaptation is 35 p.c. The nature of this change is revealed already by a closer examination of the two records in Fig. 3. After light adaptation large negative "notches" can be seen to initiate the reaction caused by the individual flashes, and the positive peaks also have become sharper. This again is best seen at the end of the records where the rate of stimulation is slower, so that the effects of the individual flashes can be separated. These are precisely the changes that take place in the frog's eye.

As the standard experiment on flicker and adaptation was repeated with the same bird on different days, it was noted that the differences between photopic and scotopic responses sometimes were more, sometimes less marked. This indicates that the retinae hardly can be quite homogeneous with regard to the elements responsible for the changes due to state of adaptation. A reduction of the intensity by means of filters also reduces the difference in the fusion frequency between light- and dark-adapted eyes.

The standard experiment with "gaps" of darkness gave the set of curves reproduced under C in Fig. 1. The similarity with the frog's eye is striking, the only difference being that this eye also has a considerable secondary rise left in the light-adapted state so that, after the rise at "off", the curves slope down towards the original base line of the non-stimulated eye. Often they go below it, as noted already by Piper [1911] and by Granit and Riddell [1934] with the frog's eye ("remnant negativity"). This indicates that light adaptation may leave a more permanent change behind the increase in inhibitory P III noted during stimulation. The directly coupled amplifier used in this work sometimes gives rise to a slow drift of base line making this instrument unsuitable for a study of these phenomena.

The cat's retina.

The cat's retina has both rods and cones, though it is dominated by rods. Zürn [1902] finds from 6 to 10 rods for one cone, but Schultze [1866] states that the cat has 2 or 3 times more rods per cone than the

human eye. Now, in the latter, according to Chiewitz [1889] there are from 15 to 18 rods per cone in the peripheral parts, so that in the cat's eye there would be from 30 to 50 rods per cone. In a paper devoted to criticism of Menner's work [1929], Murr [1930] mentions that he is about to complete a study based on some 20 eyes of cats and that he can confirm the findings of Schultze. It is certainly my own impression also of the eyes that I have stained that the cat has very few cones. Chiewitz [1889] states that even in the area centralis, where there are more cones

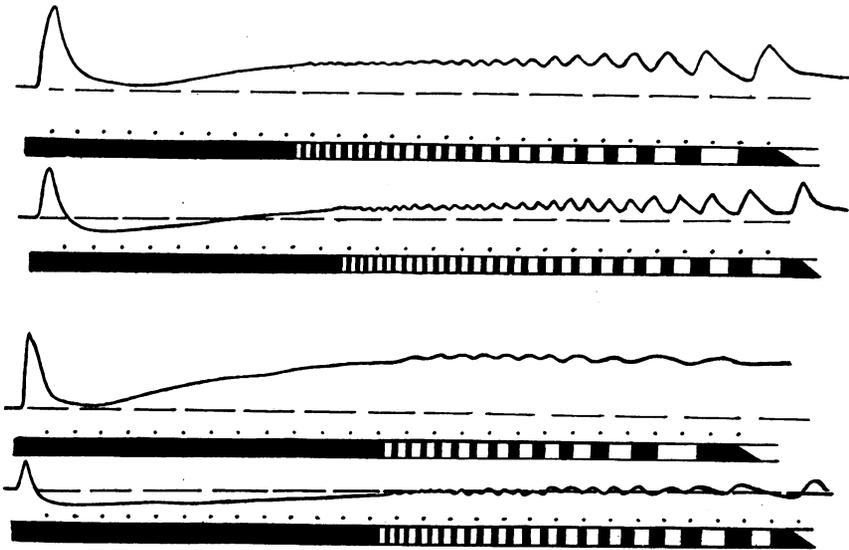


Fig. 4. Cat's retina responding to intermittent stimulation. Marked as Fig. 3. Upper pair of curves: standard intensity reduced by 1/10th. Lower pair of curves: standard intensity of stimulation. In each pair of curves the upper response is obtained in dark adaptation; the lower one in light adaptation.

than elsewhere, rods dominate the picture. In the area, according to the same author, there are 11.5 receptors to 1.2 ganglion cells, 3 mm. towards the periphery already 135 receptors to 2.5 ganglion cells. As in all mammals and in nocturnal birds the rods end in knobs and the cones in dendrites.

From previous experience with the retinal action potential of decerebrate cats [Granit, 1933; Creed and Granit, 1933] I knew that a normal maximal *b*-wave should be of the order of magnitude of 0.6–0.4 mV., but I had certainly not realized how important it is to have a scotopic *b*-wave of this size until I undertook to use the degree of light adaptation

given by the bright standard light used in this work. In the dark-adapted state the potential could be perfectly normal in outline, despite the diminished initial *b*-deflection, but after light adaptation there was hardly any *b*-wave left, and the rest of the retinal response was a slow negative swing below the base line to which the string returned at "off". The flickering waves were then very small and slow (see lower pair of curves, Fig. 4). Similar reactions are obtained when the scotopic animal is asphyxiated [Granit, 1933] after removal of P I by anæsthesia. Asphyxia removes the rapid excitatory component P II responsible for the *b*-wave. At the same time the reaction to flicker diminishes and ultimately disappears [Creed and Granit, 1933]. The frog's eye, on the other hand, gives fairly rapid flicker despite removal of P II to the extent of leaving an almost pure negative P III as the only result of stimulation.

Even with to all appearance normal retinae of decerebrate animals, as with the cat under "dial" and with one kept on artificial respiration, it was obvious that the standard intensity was above the physiological upper limit for this rod-eye. This is shown by the lower pair of curves in Fig. 4. In both light and dark adaptation the flickering undulations are small, just as in an asphyxiated retina, and it has only been necessary to reduce the intensity by 1/10th (upper pair of curves) to get brisk undulations of the type published by Creed and Granit [1933].

If the lower intensity of 62 metre-candles be used with an animal giving a full-sized brisk potential on illumination, there is a small rise in the fusion frequency after light adaptation. With this intensity the fusion frequency in the scotopic state averaged out at 26 flashes per second and rose to 27 after light adaptation. Only in one case, the one shown in Fig. 4 (lower pair of curves), was there a definite rise after light adaptation at the higher standard intensity. This is the case in which artificial respiration was given. When all 55 observations at both intensities are averaged the fusion frequencies are equal in light and dark adaptation. In other respects, however, the retinal response changes after adaptation to light. The secondary rise, chiefly due to P I, diminishes considerably, and so does the *b*-wave, especially at the higher intensity (lower pair of curves, Fig. 4). The off-effect, which in the scotopic eye only is a retardation of the fall in the response after cessation of illumination, may be slightly enhanced in the photopic state, but the change is never very conspicuous, and often the off-effect is merely a slow rise towards the base line from a small negative potential marking the final result of stimulation.

The cat's retina belongs to the E-type. This should be evident already from Fig. 4, where, despite light adaptation at two intensities, the intermittent waves always are made up by pure positive potentials. The final demonstration of the E-character of the cat's retina again is given by the standard experiment with gaps of darkness (Fig. 1 D). The light reappearing superimposed upon the off-effect causes a positive wavelet. It is particularly instructive to compare the results of this experiment in owls (Fig. 1 C) and cats (D). Both animals have a large number of rods, and in the scotopic state react with electric responses, so similar that it is difficult to tell them apart. But after light adaptation the owl has a large off-effect, an increased fusion frequency, intermittent light elicits negative wavelets, and the first effect of a flash of light on the off-effect accordingly is negative. In the cat's eye the off-effect remains small and slow, the fusion frequency hardly changes at all, intermittent light only elicits positive wavelets, and the first effect of a flash on the off-effect is positive. Yet the intensity is high enough to allow of a maximal negative component P III [Granit, 1933], in fact, too high for the cat (atropinized eye) which probably uses its efficient mechanism for pupillary constriction to keep its eye permanently dark adapted.

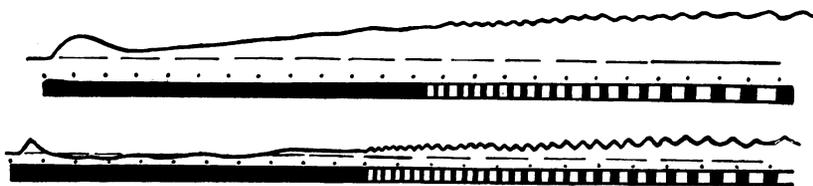


Fig. 5. Rabbit's retina responding to intermittent stimulation. Marked as Fig. 3. Upper curve, dark adaptation: lower curve, light adaptation.

The rabbit's retina.

This also is an E-retina from the functional point of view, and histologically it appears to be dominated by rods [Schultze, 1866]. There is little to add to the results obtained with the cat's eye. Fig. 5 shows the outcome of an experiment with the standard intensity. The rabbit's eye seems to stand this intensity better than the cat's retina. There is also a more definite rise in the fusion frequency after light adaptation. With the standard intensity the fusion frequency rose from 30 to 32 after light adaptation, with the 10 times lower intensity from 29 to 31. This change was regularly present and with 49 observations averaged out at about 6 p.c., calculated as above with the other eyes.

A definite negative wave could not be seen in the standard experiment with gaps of darkness. As "dial" diminishes the retinal response it is difficult to be certain of small changes. A diminished response naturally means an increased instrumental threshold.

E- and I-retinæ defined.

The I-retina is characterized by:

- (i) The relatively large and brisk positive off-effect.
- (ii) The supernormal negative *a*-waves ("notches") elicited by flashes falling on the eye during the off-effect (for details, see Granit and Riddell [1934]).
- (iii) The reaction to fast intermittent stimuli: positive off-effects, elicited by the dark intervals and cut down by the negative *a*-waves caused by the flashes.
- (iv) The fact that, when the type of reaction changes after light-adaptation, this change is better marked at "off" than at "on" and tends to make the features, summarized above, more obvious than in dark adaptation.
- (v) A fairly high fusion frequency in the photopic state.

As the negative "notches" or *a*-waves, which play such an important role in the reaction to intermittent light, coincide with inhibition in the optic nerve [Granit and Therman, 1934] the I-retina may be said to flicker with volleys of inhibition interrupting the rebound of excitation at "off".

The E-retina is characterized by:

- (i) The small and slow off-effect.
- (ii) The subnormal positive *b*-wave, elicited by flashes falling on the eye during the off-effect.
- (iii) The reaction to intermittent stimuli: repeated subnormal *b*-waves, elicited by the flashes.
- (iv) The fact that, when the type of reaction changes after light adaptation, this change is better marked at "on" than at "off".
- (v) A fairly low fusion frequency in the photopic state.

As the subnormal *b*-waves coincide with volleys of impulses in the nerve this retina may be said to flicker primarily with volleys of excitation. The work on the components of the retinal response [Granit, 1933; Granit and Riddell, 1934] indicates that the inhibitory component P III is slower in the E-retina than in the I-retina. It is perhaps altogether less important in the former type of eye.

The diagram of Fig. 6 illustrates the difference between E- and I-retinæ with regard to flicker. It begins to the left with the end of a continuous stimulus (black), eliciting a retardation of the fall at "off" in the E-retina (upper curve), and a brisk off-effect of short latency in the I-retina (lower curve). The next flash (black) evokes a *b*-wave in the E-retina and an *a*-wave (negative "notch") in the I-retina.

It is, however, both reasonable and necessary to assume that the E- or I-character of a retina never is quite pure, that just as with regard to rods and cones most retinæ really are "mixed" ones, even though one

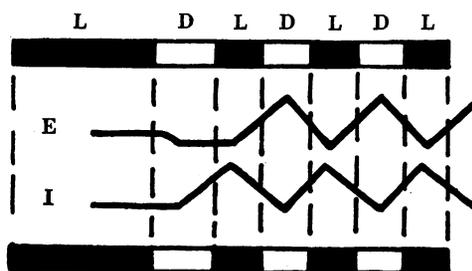


Fig. 6. Diagram, fully explained in text, showing mechanism of flicker in E- and I-retinæ. *L*, light phases; *D*, dark phases.

type of receptor may be dominating, so the concepts of E- and I-retinæ to some extent must be regarded as abstractions derived from "mixed" types. Among the animals studied the cat and the pigeon probably are the purest types.

From this point of view let us briefly consider the diagram of Fig. 6. If E- and I-reactions were present in the same retina it is obvious that differences of phase may lead to complex phenomena of interference. But rarely, if ever, can one expect negative and positive beats to cancel out as they would do if the E- and I-retinæ of the diagram were combined into one organ, but one may get smaller and larger beats alternating and changing in size in close dependence upon the frequency of the intermittent stimuli. Granit and Therman [1935] have shown that such phenomena actually are obtained both with the retinal action potential and the beats of impulses in the frog's eye. This intricate problem may have to be developed along the lines suggested by the diagram.

DISCUSSION.

The main question to discuss is whether E- and I-retinæ can be identified with respectively rod- and cone-retinæ. As we have reason to believe the retinal action potential to be localized in the synaptic layers of the retina¹ [Granit, 1933; Granit and Therman, 1935] it is important to remember that anatomical facts suggest that the synaptic paths are different structural entities dependent upon whether they begin with rods or with cones. Thus there are more amacrine cells in cone-retinæ, more horizontal cells in rod-retinæ [Ramón y Cajal, 1933]. In a wider sense then the receptor would be defined as a rod or a cone *plus* the particular kind of synaptic connections that belong to either type of end organ.

Against the hypothesis that E-retinæ are rod-retinæ and I-retinæ cone-retinæ can be advanced the possibility—to be kept in mind—that the owl's retina has just as many cones as the retina of the cat, whereas on our theory, and, in keeping with available evidence, the owl's retina should have a greater number of cones than the eye of the cat. Some caution is also suggested by the fact that the I-retinæ have all belonged to amphibians and birds, whereas the E-retinæ have belonged to mammals. On the other hand, there are sensory data available from the human fovea and periphery [Lythgoe and Tansley, 1929] which show that with regard to the change in fusion frequency with state of adaptation the fovea behaves like the pigeon's eye, whereas the periphery behaves like the eye of the owl as on our theory fovea and periphery should do. Thus the peripheral fusion frequency may drop during dark adaptation by some 30–40 p.c. (cf. 35 p.c. in the owl's eye), whereas in the centre the drop is only about 10 p.c. (11 p.c. in the pigeon's eye). We have yet to discover an E-eye capable of reacting like the human periphery. It seems, however, as if, for the time being, the objections to the theory were significant enough to warrant continued use of the neutral terms E- and I-retina and EI-retina instead of referring directly to the electric properties of rod-retinæ, cone-retinæ, and "mixed" retinæ.

¹ G. A. Fry and S. H. Bartley [*Amer. J. Physiol.* 1935, 111, 333] have recently put forward an experimental criticism of the argument that interaction evidenced by the retinal action potential shows that the latter is localized to some synaptic structure in the retina. They interpret their results as a demonstration of "stray light" simulating interaction between adjacent retinal areas. But as no precautions have been taken to exclude stray light, the results, in my opinion, may just as well be interpreted as demonstrating that interaction simulates the effect of stray light. In fact, preliminary experiments in this laboratory with excised opened eyes of frogs and exact focusing of the stimulus on the retina indicate that the latter interpretation is the correct one.

The main arguments in favour of identifying E- and I-retinæ with respectively rod- and cone-eyes are: (i) that the eyes of frogs and owls in the dark-adapted state react very much like E-eyes, whereas the I-character comes to the fore after light adaptation; (ii) that the I-character is permanent in the pigeon's eye which is completely dominated by cones, the E-character permanent in the eye of the cat, dominated by rods. The very marked changes in the fusion frequency with state of adaptation would thus occur in "mixed" retinæ. If the cones were very scarce it is probable that the fusion frequency of an E-retina would fall during light adaptation. In this laboratory Charpentier [1935] has recently been adapting albino rats to bright daylight. The retinal action potential diminishes so as to disappear among the baseline irregularities, which clearly must mean a reduced fusion frequency. These results with the rod-eyes of non-narcotized intact rats confirm the conclusions reached above with the cat's retina and very definitely suggest that a rod without visual purple is blind or almost blind, thereby providing an answer to an old question in visual physiology.

The conservative line of thought, to which I have adhered, utilizes and expands the concepts of the duplicity theory. But one fundamental and striking fact has so far remained unexplained: why is it that the large inhibitory component of the light-adapted I-retina does not appear in the dark-adapted state? Or in terms of fusion frequency: why cannot the rapid properties of the cones and their synaptic connections break through the slow rod reaction of the dark-adapted eye? The stimulus has been of constant strength and far above the thresholds for both rods and cones. The question is merely pushed one step further if it be answered that there must first take place some bleaching of visual purple with consequent diminution in the activity of the rods. On the theory that the E- and I-properties have to do with rods and cones respectively it is necessary to conclude that during dark adaptation the rods have suppressed the activity of the cones. Sensory evidence could be put forward in support of this view.

But the fact itself, of course, is independent of any theory regarding the nature of E- and I-retinæ. As soon as it has been established that in certain types of eyes light adaptation is necessary for fast flicker and I-reactions, a new factor in adaptation has been shown to exist. It can be connected with the duplicity theory only by means of some argument of the type, outlined above, necessitating the assumption of interaction between the synaptic connections of rods and cones and thereby presupposing that the retinal action potential is localized to the layers inside the receptors.

SUMMARY.

The retinal action potentials of pigeons, owls, rabbits, and cats in response to intermittent illumination with a standard light of 620 metre-candles have been recorded in light and dark adaptation with a string galvanometer and a directly coupled amplifier.

The fusion frequency falls in dark adaptation, except in the cat's eye, where the drop is absent or insignificant, if present. The fusion frequency drops in the various types of eyes by the following amounts: in the pigeon's eye by 11 p.c., in the owl's eye by 35 p.c., in the rabbit's eye by 6 p.c.

The nature of the reaction to flicker in the two states of adaptation has been analysed in terms of the components of the retinal action potential. It has been possible to distinguish two types of retinae, E-retinae and I-retinae, the properties of which are summarized on p. 434.

In the discussion the electrophysiological concepts of E- and I-retinae are confronted with the views of the duplicity theory on adaptation.

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