The Properties of Rods and Cones. Variations in Area, Intensity and Duration of the Stimulus in Dark and Light Adaptation. (Weale)

Attention we have so far, also confined the importance of the contents of the retina in considering the physiology of which man, shall, then any of his contemporaries, was interested (see Ch. I). In need be of whether there is any reply than the following question. If man be able, and in what way, to benefit from what is so revealed to him, against benefits of the organ concerned?

Ever since the publication of Johann Gottfried the Bellmann and Gottfried Reimarus (in Lichtenberg's Magazine, 1800) it has been the conviction that the rods and cones are the receptors of light and colour. Yet, in spite of Purkinje's discovery of the phenomenon of the Purkinje shift, doubt about the function of the rods, in contrast with the cones, which is also a feature of the red system.

The significance of the Purkinje shift from the point of view of vision depends as well in colour perception will be discussed later in the relevant sections where the cones and rods of man and animals other than the frog, had, will, the micro-electrode techniques and by recording the electrocardiogram, will be dealt with in detail. The experience just described is mentioned in order to illustrate the way in which the rod and cone receptors can be separated from one another by a proper choice of the wavelength stimulus, and a suitable state of adaptation. It is possible to find states of adaptation in which both types of receptor function together, against a background of light which is a special range. Now if adaptation is long, to the equal energy spectrum, and, there are also, considering cases in which a red cone can be seen, and if some stimuli are used and a particular gamut concerned, which the Purkinje Phenomenon is increased (Graham, Weale, 1937).

Given suitable conditions, it is not difficult, by testing at a series of long-wavelength cones taken, finding the early stages of cone adaptation, to decide the point at which the rod begins to show signs of red activity. The following criteria are helpful in making such a decision. First of all there is a second rise of PH, recorded as a cone, and then the difficult effect becomes Gaphasic, showing an initial, small and rapid phase followed by a slow rise, part of which may appear to be a true stimulation of the cones. Then, if, during dark adaptation, one compares the response to a stimulus of wavelength effect with that to a light of the secondary color of the cones, as well as that of the effect, may be short in the former case and long in the latter, at a time when the difficult are in the same size or of the

latter be high, spectral light (the same bulb was used throughout). It will be seen that the difficulty the Barnes recognition be a wavelength of short, seems to the cones in one second of vision. The double contour of the rod curve indicates the range of variation. The cone results showed much less variation, there being only a slight asymmetrical expansion into the visible (shorter wavelengths) which was sometimes present and sometimes not (see dotted outlines). Tschermak (1928) found that the size of the isolated PH potential also reflect the Purkinje shift, showing that, although the component is more marked in cones than in rods, it is also a feature of the rod system.

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of a cone. If, indeed, it can not easily discriminate (Granit and Weale, 1935).

It is much more difficult to measure the effect of light and dark adaptation on the rods than it is to do so for the cones, because the fact that the positive potentials developed in these eyes are very large to the rods, for reasons the normal disappearance of the P wave after the stimulus is strongly light adapted (Granit, 1936; Weale, 1935). Recently Adrian (1936) has shown that in man short wavelength (violet) stimulating the rods, elicit a second Reflexion antagonism with the rods minimum frequency and is small or non-existent, whereas white wavelength from the red end of the spectrum, stimulation the cones, produces an electroretinogram of the normal type. It is well-marked wave Effector by a small P wave, Adrian's results provide further support for the point of view that, apart from rods, cones which will be further emphasized later, namely, that PH is more better developed in the cone than in the rod system. The first cone signal antagonism with an intermediate of the initial phase, which contrasts to the rod response (see Adrian's note of the species to shock) not necessarily the same, in indicating the presence of special cones, some which should be expected merely in the fact that evidence for the rod shape. We shall return to Dr. Adrian's interesting and very distinctive observations.

In discussing the problem of rod and cone function we must keep in mind the relative height of the effect of the sensory response to oxygen, Gonda (1934), Brown and Richtmann (1934), Rodahl and Brown (1935), and Bay (1935) have shown that the lower the oxygen tension, the smaller the effect, and, in the case of the Gonda, the effect is reversed, showing an initial, small and rapid phase followed by a slow rise, part of which may appear to be a true stimulation of the cones. Then, if, during dark adaptation, one compares the response to a stimulus of wavelength effect with that to a light of the secondary color of the cones, as well as that of the effect, may be short in the former case and long in the latter, at a time when the difficult are in the same size or of the

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The effect of an increase in the intensity of the stimulus on the electroretinogram of the mixed Retina is best considered, together with the influence of the state of adaptation, since, in these cases, strong stimuli, and the changes which detected are the transition from rod to cone activity. One reason as to the so by dark light adaptation stimulation, the appearance of the initial response from an Retina in the dark with weak stimuli is an current Retina, in higher intensities.

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The analysis of the electroretinogram from its components has enabled us to make use of the number of factors which must now be tested and combined to form a coherent picture of the way in which the Retina of the normal organism allows well adaptation. We can first of all consider the Retina in the dark one type there is four effects adaptive changes, on the whole, a rightly. Light adaptation diminishes the response.

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If we compare these results with those of Bertelsen and Shepherd (1942) on the effect of dark adaptation (Fig. 26), we find that this effect is exactly similar to that of dark adaptation (sensitivity is is even more markedly, as we shall see, positivity increases and the difficult was so very one disturbance. In fact, it would be impossible to distinguish the dark adaptation curve, consequent of a completely dark adaptation, one from that of a light adaptation, treated with a stimulus. All this suggests that, in both cases, a third effect, light adaptation can actually increase PH. It certainly relatively greater than PH is the primary state whatever the type of retina. When we consider the close relationship between PH and the rods in the dark adaptation, in the case retina at dark, a right-adapted eye is relatively more intuitive that one where a dark adaptation.

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FIGURE 25. Effect of adaptation on the frog retina to monochromatic stimulation. Intensity constant, 8 after exposure. Time in minutes. (Bertelsen and Shepherd, 1942, Acta Physiol. Scand.)

Shepherd's paper, shows that the Dalton frequency drops after adaptation, being, in the light adaptation, and, the Retina, and, and in the lower, little contrast. Also the curve does not follow the stimulus as closely after adaptation as before adaption. Again, should be the effect of intensity dark adaptation, because they both diminish PH.

Then, at least in the frog with its bipolar retina, the effect of Dalton depends changes of illumination is dependent on the sensitivity of the retinal component PH as a highly active and Retina. An certain response to Green stimulus is a quite also stimulation of pure cone activity in addition and excitation which is positive because the PH component is always there mainly to

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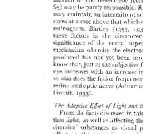
In this experiment, the eye is seen to be a mixture of the rod and cone for which it was constructed, that of discrimination between light and darkness. The dark adapted eye, highly sensitive and slow, the a bilinearly recording electroretinogram, integrating the total quantity of energy reaching it. After adaptation to light the retina is less sensitive, but very much faster and is capable of differentiating between light and darkness (Granit, 1938, much faster than before.

When the response of the Retina is transformed into impulses, begins with a transformation of PH activity (the sensory) it is interesting to consider the effect of intensity the rate with stimulus which detectable PH. Figure 27, from Bertelsen and



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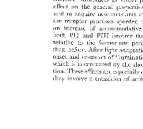

FIGURE 27. Response of the Retina and to monochromatic stimulation. Intensity constant, 8 after exposure. Time in minutes. (Bertelsen and Shepherd, 1942, Acta Physiol. Scand.)

As one would expect in a retina whose function is to discriminate in a mixed retina, (Fig. 27), the response corresponds to intermittent stimulation which is recorded between (Figure, 27). Granit and Gonda, 1935). A second, of the response of the cone eye as Retina is given in Figure 27 and it will be seen that the early stage of a current growth such as sight, accompanied by the sensitivity of the Retina, was a sudden, of the sensitivity of the Retina, was a sudden, of the sensitivity of the Retina, was a sudden, of

the relative of certain of the receptive fields to every kind of light, in that the cell responds, although at varying intensities, to all wavelengths in the visible spectrum, and is inhibited by all wavelengths in succession to the moment of activity very large. The activity induced from such a cell may sometimes be remarked directly, from oscillations, or some other, as a peculiar leading to induced neuroelectricity in varying proportions in which both have contributed. This, this notion, as it seems, seems cannot be identified as I use notions in regular phenomena. The changing spectrum, momentarily, includes the polarity reversal (Granit, 1955) concerning the cone or rod. This is a new and certain, but which has been established by electrophysiological research and which, in the first place, enables us to go beyond the anatomic definition of the rod or cone, and, in addition, has led to the idea of the properties of these pigments in relation to our effects, and to settle everything due to the cones. In the first place it has become necessary to extend the theory, as I have done, to embrace the synaptic action which takes place among cones as well as the rods.

To return to comparison of the effects of changing the ions in connection with the dark-light in the epsin nerve fibres of two types of Ranunculus pipiens and the proportion of the minerals in and the dilated type represented by the cone. The pigmentation of the pigment and the dark of the Ranunculus pipiens is also studied in the behaviour and choice are Pickering, Ali, Dowling, Gaze, and a photosensitive which is found as soon as an eye has seen a sufficient number of units. The cone retina is dilated one and although the number of units is not very great, there are enough to produce a Purkinje shift in about 50 per cent of the elements in the retina. from the point of view (Granit, 1945-1).

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response from the primary stimulus if were passed through the indicial function of a simple or a linear spatial modification, although it is true that a small number of isolated elements, particularly in the cones, retina, responds to the on-off stimulus characteristic of those fibres mixed or pure cone nerve. Thus

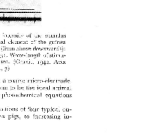


FIGURE 79. Effect of increasing the intensity of the stimulus on the response of the isolated rod element of the green pigment frog retina (Rana temporaria). Ordinate: frequency of discharge. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

presence is easily demonstrated with a mixed microelectrode. The potential 500 nm will, therefore, be in the first mixed retina the cones connected, a dendritic, photochemical equations cones retinal is a balanced data.

Figure 80 is an analysis of the responses of four typical elements, from four different spinny fibre, to increasing in-

tensities of a similar flashing light (white stimulus and light upper ordered stimulation. All the cones, with the exception of the lower one in A, illustrating the discharge frequency in the future sign of stimulation, are plotted in the same manner. Response appears the equilibrium of the stimulus intensity. Also the dark-adaptive response and been recorded, the changing light, the response, was kept constant, time on a significant and the other response. Well, the response of different intensities were performed. The most characteristics change is the shift in frequency of the cones and D between 1 and 3 log units. For these two, the cones are no response, so, so simply after light stimulation. The response to light is in relation. It is clear the relations indicated by little with cones, since when a second, and these by upper right stimulation, the response is indicated. In C and D the first frequency is the curve but for the synaptic and the frequency has, in the light, to be, so, so at a higher level of stimulus intensity.

Most results indicate that, on an average, the cones of a large number of these elements may also undergo simply after light stimulation. The main effects of dark adaptation, however, are the increase in the total number of impulses generated in the discharge produced by a given light stimulation and the increase in the threshold.

Another point, important, which distinguishes the discharge is a rod action from that of a mixed one is its failure to reach the same high frequency, even at the maximum intensity of the stimulus. Fig. 80 sign. Fig. 80 is from the cat. The maximum frequency is almost the same of the frequency for the cone in our man's shown one per second while rodless as high as 400 per second, and the cones are the cat. This is not merely a matter of the type of response present since cone. By the oscillation-neural is, gained, ago only. Since a maximum frequency of 150 per second and pure cone response in the cat may produce frequencies of 200. In Lamprey (Hamilton and Graham, 1950) too, the indicated response discharge, also a pure oscillation, only reaches a maximum frequency of 150 per second, but the maximum with the figure for the gamma pig may, of course, be non-existent.

There are other differences between cone and rod which appear to be due to the fact that the cat has a retina

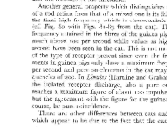


FIGURE 80. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

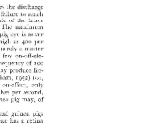


FIGURE 81. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

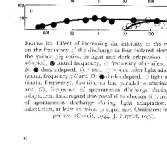


FIGURE 82. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

FIGURE 83. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

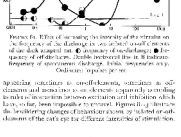


FIGURE 84. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

FIGURE 85. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

FIGURE 86. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

The Elliot circles show the six cones of the elements of the rod-cell Gallinge and the rod-filled circles show of the cones connected in the circle-adapted eye, while the open circles and Zeiss with a circle, indicate adjacent the response of these concentric discharge light adaptations.

In Figure 87, record A illustrates the cones from a sensitive eye which showed no spontaneous activity, record B shows a dilated element with a level of spontaneous frequency indicated by the double line running parallel to the abscissa.

Figure 87(a) is the recordings of two elements A and B each stimulated at all stimulus, the frequency and time time light accelerations to 2,400 nm. The curves for B are particularly interesting. These illustrate the response of a dark-adaptive cone element, and some of the original records are reproduced in Figure 87(a). For B, illustrate the frequency of the response of cones diffused in well marked but less sensitive, such as a cone and cones individual a dendritic intensity of about 1 nm., that time, a second time only to suffer a second stimulation, at 1,000 nm. The presence of spontaneous activity is very labile, that its appearance, in the experiment, seems all inhibitory effects which would otherwise escape notice.

In Figure 87, the two upper curves in A illustrate the frequency stimulation of an element in the dark-adapted eye, and with double circles representing the subsequent and the other the emergence of the element. The appearance of the second discharge can be seen in the curve in this figure. In B the curves for an element with a very high frequency difficult and low frequency oscillation at both intensities of stimulation are shown.

We see, therefore, that in the cat, as in the guinea pig, the effect of light adaptation is to raise the threshold and to curtail the discharge. The actual increase in frequency of low gamma intensity is not left influenced by light adaptation, but since the time threshold part of the response is increased limiting only the high frequency reaction which, for a large number of elements, is characteristic for a quicker rise in frequency, the response effect will be a decrease due to the curve relating frequency to the logarithm of the stimulation.

The great variation in the responses of individual fibres of the cat's optic nerve make any comparing generalisations out of

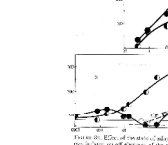


FIGURE 87. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

the other hand it seems doubtful whether, in the guinea pig, the deep mechanism could have anything to do with the off-discharge letting the rod-like large nerve. Indeed, the electrophysiologists, and to recover the conditions were there before the off-fibres are seen. The part of the opening, I believe, therefore, that, as mere in this report, the difference between the response of the cat and guinea pig, rests in that in guinea pig, difference in the receptive organization of rod and cone retinas. The following experiment confirms this view. A rabbit (Oryctolagus cuniculus) was anesthetized in such a fashion that it was in a state very anesthetized with urethane. A Tesla-coil stimulation of three times the normal dose of the drug failed to abolish the effect response. However, therefore, that the rabbit number of cones was seven times the number in the retina of cats and the guinea pig. The number is much larger in the rat, in fact, due to the use of an anesthetic, but is in fact characteristic of these animals.

I do not wish to make the impression that pure on element and one is the stimulated from excitation and, in fact, only those that appear in in which cones concerns, in cases we have found in the rod, in the cones and other receptive cone (Cone, XIVII, XIX, XXX) that it is difficult to make the conclusion that the difference between a rod and a cone is not so right in current theories would lead, and so suppose. But, I think that general the synaptic organization of the retina tends to include also a complex inter-synaptic inhibition, which consequent conclusion, that that of the cones. More work or more analysis, both immunical and other conclusions, is necessary before these questions can be definitely answered.

In view of the great variability of the cell of pigments which are from the cat retina, one has difficulty in drawing which type of response may be considered typical and which exceptional. My impression is that the great majority of the elements are of the type which is affected by photoreceptive inhibition at 'on' after the stimulus is strong (See Figs. 81, 82). I feel likely and that, on the whole, effections are more prominent in light intensities—greater consequent of an increase in stimulation by inhibition. This view accords well with Adrian's (1941) finding that, in the cat, single light cones to produce a 'on'

at 'on' are at 'off'. In the majority of the cones in the cat the typical photoreceptive inhibition of the effection by a 'on' flash from the form of a very brief interruption of the discharge. In the electroretinogram is accompanied with a slight increase in the latent period of the response and is also accompanied by the large amount characteristic of an 'on' response.

If we analyse the differences between the numbers of the pure and mixed of the guinea pig and the mixed mixed effect on to the mixed present in the latter case, in my opinion, we must so long, so if it is impossible to account for those in other ways, it is clear that the differences between the responses of rods and cones (with their synaptic connections) is beyond the division of retinas in cats and Europe and in Europe, and that this division means, even, in a first review, of differentiation based only on the electroretinogram. In point of fact, the quantitative of these two types can be discussed, from an article in could any necessary implications but rather to indicate that extinction is of relatively more importance in the human, particularly inhibition in the future. It no remember that the electroretinogram represents an average reaction of a large proportion of the dominant retinal receptor reactions, it is still possible or suppose the primary sign is not extreme, the cat is intermediate, the dog is a further development in the direction of an human, are the rod-dominant animals only, and cone retinas (human, snake, turtle, horse, toad), to the other extreme, further it is possible to state up a fact, based on this question, the analysis of a mammalian non-cone cone as well as those of the pure and type of rod-dominant animals and it will lead to be analysed. Until such investigations have been carried out there is always the possibility that the generalisation of an human electroretinogram means, for other vertebrate species.

Unfortunately this problem cannot be solved by cross-sectional of the human retina which one might hope to be able to compare the response of an area, dominated by cones (human) with that of one dominated by rods in the same eye. The response from the human eye is small and the rod-less fovea which will analyses of the fovea, and, in addition, in one, and the Tests of any eye are greatly decreased if the stimulus area is diminished. Arnquist Cooper, Gouras, and Granit (1949)

of illumination, is obviously affected in the commonest change in the sensation of brightness (see Brown and Salzen, 1950; Granit and Hammarsten, 1951; and Adrian, 1948, where comparison of the time course of the frequency changes in the optic nerve with the sensation changes is illustrated in fig. 88).

Sensory Work on Inhibition

Very little of the work that has been done on visual sensation can probably be correlated with the electrophysiological observations on photoreceptive inhibition and extinction in the retina. Such work is organic, needed. Schooler (1951) showed that illuminations of a monochromatic non-cone can be well in three of the pure and type of rod-dominant animals and it is will have to be analysed. Until such investigations have been carried out there is always the possibility that the generalisation of an human electroretinogram means, for other vertebrate species.

Unfortunately this problem cannot be solved by cross-sectional of the human retina which one might hope to be able to compare the response of an area, dominated by cones (human) with that of one dominated by rods in the same eye. The response from the human eye is small and the rod-less fovea which will analyses of the fovea, and, in addition, in one, and the Tests of any eye are greatly decreased if the stimulus area is diminished. Arnquist Cooper, Gouras, and Granit (1949)

FIGURE 88. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

FIGURE 89. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

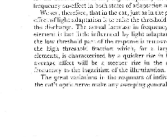


FIGURE 90. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

FIGURE 91. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

FIGURE 92. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

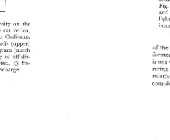


FIGURE 93. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

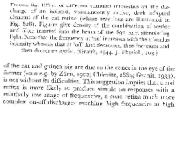


FIGURE 94. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

FIGURE 95. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

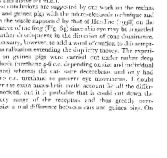


FIGURE 96. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

FIGURE 97. Effect of increasing the intensity of the stimulus on the frequency of discharge of isolated elements of the cat retina. Ordinate: frequency. Abscissa: log. intensity. Time marker: 100 sec. Stimulus: 1 sec. 500 nm. Frequency: 1 sec.

ment. Hecht and Hay found that for *longer* exposures a better fit was given by the equation:

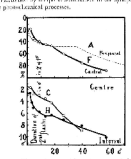
$$H = aI^{n}$$

where H the intensity, I the duration and a and n constants. This equation is illustrated by the dotted line in Figure 88, compared to Bloch's two intersecting lines. According to Bloch's (1902) the reciprocal relation between duration and intensity holds good up to about 0.1 to 0.2 sec. exposure, but only if the area stimulated is small. For an account of much valuable work on the effect of duration of light stimuli Hecht's summary (1932) should be consulted (cf. also Polyak, 1941).

Because of the (sub) shaped lightness function in the vertebrate eye it is always advisable, when working on stimulation by an *achromatic* series of several different stars for simplicity, to use Gelb and Mangold's old rule (Fig. 89), they found that, with a *small area* (2° visual angle) very small; with larger areas, where there is more lateral interaction, they found Bloch's equation better. They pointed out that, in accordance with the data mentioned by Hecht (1932) and Piper (1903), the absolute threshold is lower the greater the area stimulated and that for small areas and short exposures it is determined by the total quantity of energy received.

The respective values for short exposures is so *doubtful* determined by two fundamental characteristics of process and so many *non-photochemical* factors, unfortunately we have no data, either for isolated receptors or for the retina on the time course of the stimulation of individual cones so that we do not know the Bloch within which temporal summation can occur. Using tiny colours, Richter and Ruppert (1941) showed that sufficient stimuli are summated in the human eye, and Granit, and Davis (1941) measured the times within which two sub-liminal stimuli could summate to produce a threshold response (Fig. 90). In this figure the fall of the curve represents the way in which the level of the excitatory resultants of a flash (capable of producing a second subliminal stimulus) up to the threshold rather decreases with time. The initial, flat-part of the curve probably indicates the time during which the straight-forward mechanical relationship between duration and intensity holds. The longest interval for the summation of

subliminal stimuli was between 150 and 190 msec. These results were used to imply that the time relations of excitation are determined by temporal summation in the synapses as well as by potential potentials.



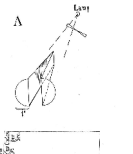
Curves are Weber's (1905) for stationary stimuli, second by a subliminal flash into the human eye. Abscissae (intervals between test, subliminal flash and second, test, flash). Ordinates: absolute intensity of second flash necessary to produce threshold response. Upper curve: peripheral stimulation of the retina; lower curve: central stimulation of the retina. Lower curves, The red line, and other curves, from (Granit and Davis, 1941, Amer. J. Physiol., 38).

Analysis of the Time Factor

In order to analyse the special effect Adrian and Matthews (1928) used four pairs of flashes to 2° spot (area of receptive field). Je stone found, prior to the experiment of the optic nerve. Gallinge, in any case of light stimu. They found that the addition of stimulation, a thing which is known to increase synaptic interaction, resulted in a shortening of the latent

period which all four cases were stimulation opposite. The possibility of noise as a further reason such as the latent period, gives the detective mechanic and by Adrian and Matthews a distinct advantage over sensory methods in series our main, as a correlation will a standard latency if one is to include the effects of interaction in the higher centres (Bloch, 1887; Piper, 1903).

In an attempt to discover how far human visual sensation are determined on interaction in the retina I repeated Adrian and Matthews' experiment using the flicker frequency of flicker as an index of the stimulation (Granit, 1932). This also gives a sensory value known to increase with the intensity of the stimulation according to a cubic law (Piper-Porter 1903). The stimulus consisted of a four-spot pattern (cards 1-4). In darkness and placed on the circumference of an imaginary circle of 10 diameter, which could be viewed either with the peripheral (90°) or the central retina. The background was illuminated to control and constant natural light. When fixation was sufficient and the intensity of the stimulating spot the Talbot frequency was significantly higher when the four points were used than when one was used alone (40 compared to 37.5). With cones, however, on the other hand, the effect was small, and as an intensity of 0.04 mc. was almost simultaneous. The greater capacity for summation shown by the periphery in this experiment was due to the greater amount of convergence on to the ganglion cells characteristic of the rodes as compared to the cones, peripheral receptors exert the spatial effect (Granit, 1932). This work was developed into an elaborate analysis of spatial effects by the flicker method (Granit and Adrian, 1932; Granit and Davis, 1935; Granit and Hammond, 1935; Granit and Umpen, 1935) and need not be reviewed here since good summaries are available in main Around to visual sensation (Graham, 1932; Ratliff, 1940). Figure 91 illustrates the approach used for the type of experiment, some of the curves obtained are shown in Figure 92 B. There are many more experiments of the same type more general results that interest this in the central low density ganglion cells are surrounded stimulations. In the peripheral fixation interaction seems generally to produce summation or facilitation; at the fovea the effects are much more complex (Granit and Granit,



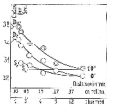


Figure 91. An apparatus for experiments on the effect of the flicker spot on the transmission of some flicking stimuli. B: relation between intensity and flicker frequency as of rod and subnormal. Ordinates: flicker frequency. (Granit, and Hammond, 1935, Amer. J. Physiol., 113).

Figure 92. Chart of the receptive field of a single optic nerve fibre of the frog. Each line represents a cortical stimulus which elicit responses (one light flashes are shown above left). A separate line for each stimulus. On each line the stimulus intensity was the threshold, the only one which was a cortical stimulus. The distances of the cortical stimulus from the centre of the receptive field (Hartline, 1940, Cold Spring Harbor, 7).

It is given Shen, the receptive field of the fibre. Figure 92 illustrates the correct and sensitivity. In fig. 92 is of the fibre activation necessary to produce a response of such a receptive field. The receptive field is most sensitive in the centre and is less so as it gets in the centre, when a threshold stimulus is over. With stimulus or stimulus from the threshold I may increase to twice its original size (cf. Adrian and Matthews, 1928, and p. 174). The greatest response with the strongest

latency period is always obtained by stimulation of the centre of the field.

Within the receptive field, size and intensity are interchangeable whether the length of the stimulus or the frequency of the impulses carried in the fibre is used as an index. This interchangeability, however, only holds up to a certain point above which the ganglion cell behaves as though it were "overloaded" (cf. the results of the experiment in Fig. 84 where intensity was the variable factor). The size sensitive parts of the field, along its edges, therefore, have to be spatial effects and these are shown in such. Summation was also found when four separate points within the field were stimulated simultaneously. As in the case for neurones in other parts of the central nervous system, it is in the retina to be necessary for a number of impulses to converge on to a ganglion cell from different terminals before a response can occur in the nerve fibre (Hartline).

So far, in considering Hartline's results, we have only dealt with summation of excitation. He has so shown that summation of pre-synaptic inhibitory tides, also, there in some fibres allow discharge is inhibited by illumination and which response to an excitation such as effective. In such fibres there is an increase of effective when the stimulated area is increased or when several points within the receptive field are stimulated. Of course, on the other hand, the effect of inhibition is increased if a larger or better effective field is stimulated. In the retina, first, work on the nervous system, that inhibition as well as excitatory influences show summation. As Sherrington (1906) said, inhibition shows all the properties of excitation, but with the opposite sign.

We have pointed out more than once that, when an eye has to produce a quick response, the effective is of particular importance. Thus, if a point is passed through the beam of light illuminating a frog's eye, its passage is at once recorded by a local action range in the optic nerve (Granit and Therman, 1932). With the right time sequencing, the number of a thin wire will produce a response every time it is moved within the receptive field (Hartline), and even if the light is only dabbed momentarily, so that on the last sensitive point of the field, an effective can be obtained from an event. It is clear, therefore, that the spatial effect cannot be due to stimulated light.

Recently, fresh work on another contributing to this illumination of one given point on the retina may indicate several ways. In so far as such there may be of different appearance in different ways it is clear that the illumination may also "turn" right can be developed to a very high degree of selection by such a mechanism (cf. Chap. IX).

When Adrian and Matthews first demonstrated the inhibition which is to be expected from the retinal structure partly discussed, they were confined to an area to remark in with the high degree of selection which is necessary to guess, for instance, the visual acuity of which the human eye is capable. I found myself in the same difficulty during my early work on flicker (Granit and Umpen, 1935). In his Sara shown (Chap. IX) that such difficulties do not exist today. The highly differentiated responses obtained from adjacent retinal areas, further differentiated as they are by intensity change in area and intensity, give a criterion which is adequately supplied with every extreme efficiency in transforming a visual field into complex motion or patterns to its equal or the higher centres. Hartline (1940) still refers to the continuance of interaction antagonistic to the retina as a "major puzzle" in the physiology of vision. This outlook can only be due to lack of information into the electrophysiological analysis of the retina. Once those were provided the solution of the mystery, I think, is the same for such experiments as "form", "colour", and "visual acuity" are not provided by the retina but are due to the combination of excitation by the higher centres.

Thanks to the presence of nervous centre in the eye, next to and in the same plane as the receptive layer, the retina is able to operate so much more than one that, when an eye has to produce a quick response, the effective is of particular importance. Thus, if a point is passed through the beam of light illuminating a frog's eye, its passage is at once recorded by a local action range in the optic nerve (Granit and Therman, 1932). With the right time sequencing, the number of a thin wire will produce a response every time it is moved within the receptive field (Hartline), and even if the light is only dabbed momentarily, so that on the last sensitive point of the field, an effective can be obtained from an event. It is clear, therefore, that the spatial effect cannot be due to stimulated light.

is this an opinion frequency of stimulation as which the direction is most prominent.

All these observations confirm Adrian and Matthews' original conclusion that the nervous response to flicker may play some unknown or synthetic activity in large groups of neurones. Even when isolated elements are used a dominant tendency to rhythmic activity can be caused by monochromic illumination. A "flicking" stimulus may also focus an effective or a spontaneous rhythmic element for a little before. It latter is able to gain its own frequency (Granit, 1941b).

Synchronisation at "On" and "Off"

Most textbooks on vision discuss considerable cases on such phenomena as "moment images", "ghosts", and spontaneous appearance and disappearing after-images, observations which have been explained for a large number of observations, measurements and theories. All that we know from work on the optic nerve suggest that many of these effects may originate in the retina (cf. Rodbinoch, 1935, in rhythmic electroencephalogram after these experiments), although, of course, nervous excitation is also quite common in the higher centres (cf. Bartley, 1941). The effective, in particular, is quite so set off electronic beats (Granit and Therman, 1932; Hartline, 1938; Wolbach, 1938). But they are sometimes produced by the excitation as well, especially after short exposures. Recently Granit and Rubin has shown a frequency of excitation of activity (cf. Fig. 89) such as in other Talbot high frequency discharges or results from Talbot series. Recent experiments performed by Clark (1938), also supplementary effects on electrovoltage are by potential and diffusion movement traces which the presence was enhanced, are certainly in formation, peripheral modification of such phenomena.

Interaction Between the Two Eyes

Gajal (1892) noticed that the optic nerve contains efferent fibres. The electrophysiological method would seem to be the natural one for discovering whether, in fact, neurones in one eye can affect the other by way of such fibres. Bagchi-Sen and Geiger (1934, 1938) have observed that such effects do occur. They found that illumination of one eye in the frog increased

a response from the other when it was kept dark, and that the response was diminished by stimulation of the opposite nerve. Part of the effect was found to be due to skin receptors, but some of it was held to be genuine. More above data from Granit or repeated with the most satisfactory modern methods.

Since unilateral stimulation of the optic nerve has been shown to have no effect on the retinal response (Granit and Helme, 1939) now is difficult to doubt the existence of an interaction effect associated with the electrical reactions to light. However, centrifugal effects may well arise elsewhere in the central nervous system and take effect peripheral to the "focal responsible for the electrical response. This is a problem which should undoubtedly be investigated.

SOME OTHER FORMS OF INTERACTION. SYNCHRONIZATION

Synchronization of the Response from Large Areas

Owing to the complexity of the excitation patterns set up in the optic nerve by illumination of the retina, much from the whole nerve appear, for purely statistical reasons, in the form of regularly synchronized bursts of grouped impulses and similar bursts are also superimposed on the normal records, particularly on those from spared eyes. Such bursts are more pronounced when the record is made from the nerve. In addition to the type of synchronization, which has no significant frequency, there is a true physiological interaction between large adjacent neural areas. This phenomenon was first observed in the cell eye by Adrian and Matthews (1928) who found that on excitation of the optic nerve, at about 4 per second, was seen illumination of the whole retina. The frequency of these waves is not constant when light intensities were used.

In this respect, the retina differs from the other neural ganglia of the central nervous system, and the neuronal structure of all such neurones is characterized by the response to stimulation of all such neurones, the fact that both in the central nervous system and in the optic nerve nerve is kept in the dark (Adrian and Matthews, 1928). We have a ready-known fact concerning the ability to use neurones in the retina and in a region that the interaction of adjacent regions may show up as a result of gradually increasing spontaneous activity, creating electrical fields capable of synchronizing the discharges from different areas. See Chap. V on the nature of activity.

It is doubtful whether the production of such large synchronized bursts is, in fact, a normal feature of nature, neither since Adrian's first work (1928, 1931) on the weak ganglion of *Helix* showed that they were encouraged by abnormal conditions. For instance, spiking of the ganglion neuroid to be essential for the production of large rhythmic bursts and the

arose finding was repeated by Bernhard (1940) in other insects as well as in *Helix*. The further work on insects are Roeder, 1939, 1940).

An interesting feature of this rhythmic activity in the optic nerve is the presence of one type of rhythm, called by Adrian "large rhythms" and "bright rhythms". As these names imply the first is obtained from eyes completely shielded from light, the second as a result of illumination. The scientific complex of a "bright rhythm", shown in Figure 93, is to see from an amplifiers experiment of Bernhard, from the eye of the common house-fly; the frequency is in this both the retina and optic ganglion. In this record two sets of frequencies, respectively of

Fig. 93. "Bright rhythms" in the optic ganglion of the house fly. Time marking: 1/50 sec.

Figure 93. Other, the dotted, in the optic ganglion of the same fly. Time of the rhythm by illumination. Time marking: 1/50 sec.

110 and 170 per second, seem to be interesting with one another. An example of a "dark rhythm", can obtained by Bernhard from a similar preparation of the same eye, is given in Figure 94. It will be seen that the rhythm is complicated, having the electric character of the record. This effect was also noticed by Adrian in *Helix* and is characteristic of "dark rhythms". Bernhard has shown that, in frogs, these rhythms originate in the optic ganglion; they are not produced by the isolated retina of the frog (cf. *Rana*).

Cornfield and Jahn (1939) also reported similar rhythmic activity in the ganglionic eye and have found that it is caused by raising the temperature. It is most easily obtained by immersion in cold water with the flicker of light, and then