

RODS, CONES AND THE LOCALIZATION OF  
PRE-EXCITATORY INHIBITION IN  
THE MAMMALIAN RETINA

BY RAGNAR GRANIT AND KATHARINE TANSLEY

*From the Nobel Institute of Neurophysiology, Karolinska Institutet, Stockholm*

*(Received 25 February, 1947)*

The single spike record from a retinal element or unit, isolated by the micro-electrode technique, provides us with valuable information about the message delivered by the ganglion cells of the retina to the higher visual centres. The study of such records has already made it possible not only to detect excitation and inhibition in the retina but also to analyse the sensitivities of the actual receptors to different spectral wave-lengths (see Summary, Granit, 1947).

This paper is concerned with the relationship between the amounts of excitation and inhibition produced at the threshold of stimulation for the receptors of the cat retina as well as with how these two processes are related to the reactions of the rods and cones. Such differences as we have found in the association of excitation and inhibition with rod and cone reactions can probably be related to the manner in which their synaptic connexions are made.

THE PROBLEM

The present problem may be best understood with the aid of Fig. 1. In the diagram on the right of the figure three single retinal nerve fibres (whose reactions to stimulation are picked up by the micro-electrode) are illustrated, one transmitting entirely from rods, and the other two from both rods and cones. Such a convergence of retinal end-organs has been demonstrated histologically by Polyak (1941) and physiologically by Granit (Summary, 1947) in several different animals. In the cat, most if not all of these receptor units (i.e. receptors, bipolar and ganglion cells) contain some rods (Granit, 1945), and this fact has been utilized in the work to be discussed here.

If the discharge of such a retinal element simply represented the responses of the receptors, the result of illumination would be a more or less *pure on-effect*. In practice, however, the majority of the retinal elements which we have isolated responded to stimulation with both on- and off-effects, and some even

with *pure off-effects*. This must mean that pre-excitatory inhibition (Granit, 1947) can act in some part of the complex retinal element suggested in Fig. 1 and, with more attention to detail, in Fig. 8.

Our immediate object was to discover the relationship between the sensitivity of different retinal elements to the onset and cessation of illumination and whether this relationship was the same for elements containing rods only as for those containing both rods and cones. In order to separate the reactions of the rods and cones, even when they were connected to the same nerve fibre, we

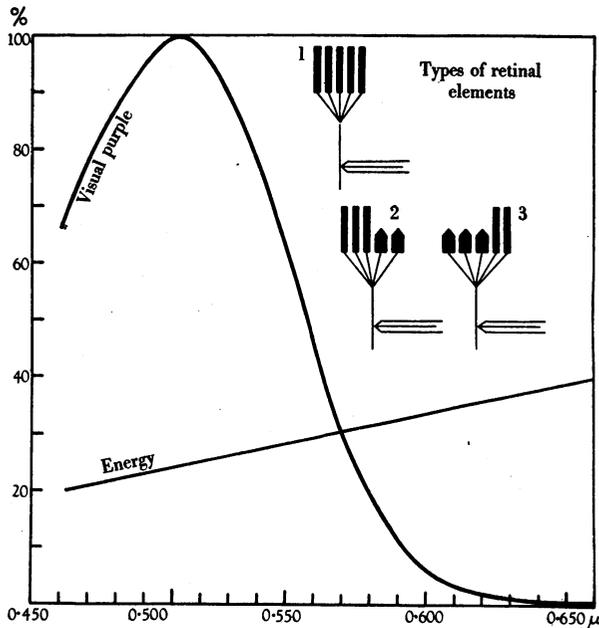


Fig. 1. Absorption curve of visual purple and schematic illustration of energy output of colorimeter lamp (straight line).

Top right-hand corner: diagram of types of retinal element postulated for the cat with the micro-electrode in position on the nerve fibre. 1, pure visual purple (rods only); 2 and 3, mixed rods and red-sensitive receptors (cones).

compared the responses to two wave-lengths, a blue of  $0.460\mu$ . and a red of  $0.650\mu$ . Since the observations were all made on fully dark-adapted cats (the animals remained undisturbed in the dark box for not less than 1 hr. after the micro-electrode was in position and before the observations were begun) in which the retinal responses are dominated by visual purple, blue is a far more effective stimulus than red. In order to detect any responses which were *not* due to visual purple the intensities of blue and red could theoretically be adjusted so that they become equally effective as bleachers of visual purple; any inequality in the response would then probably be due to other retinal mechanisms.

Our actual procedure was to calculate a correction factor for each of the two wave-lengths of our spectrum chosen ( $0.650\mu.$  and  $0.460\mu.$ ), based on their absorption by visual purple (Lythgoe, 1937), the energy distribution of the lamp used to produce the spectrum, and on the quantum intensity of the spectrum. These correction factors were adjusted so that the factor for a green wave-length of  $0.500\mu.$  (the peak of the visual purple absorption curve) should be equal to unity. When such corrections are applied, the red wave-length is found to have only about  $0.0045\%$  of the bleaching power for visual purple of the blue. This is because so much less of this wave-length is absorbed by visual purple (Fig. 1). We then measured the intensities of the red and blue which were just sufficient to evoke a response at 'on' or at 'off', and used the factors to correct these threshold values in order to ascertain whether, for any given unit, the thresholds for each wave-length were those which would be expected if the unit's response were mediated by the reactions of visual purple alone, or whether it was too sensitive either to red or to blue for this to be the case.

All our results are given in terms of these equivalent stimulus values and are expressed as red-sensitivity ( $R$ ) or blue-sensitivity ( $B$ ) where the sensitivity is the reciprocal of the threshold intensity. On this basis any given element may show  $R=B$ ,  $R>B$  or  $R<B$  for either the on- or the off-effect. An element for which  $R=B$  is, according to our correction, one whose reactions are conditioned by visual purple (probably a pure or nearly pure rod element). Where  $R>B$  special red-sensitive receptors must be affecting the response and where  $R<B$  there are probably special blue-sensitive receptors. The final balance of power between red- and blue-sensitive receptors and visual purple will be given by the relationship between the responses to red and blue. The special red-sensitive receptors are certainly cones (Granit, 1947), the blue-sensitive ones may be rods or may be some intermediate form between rod and cone. However, the situation  $R<B$  is rare in the cat retina and in these experiments was only found among the pure on-elements.

It should also be possible by analysing the relation between the off- and on-components of a responding on-off-element to obtain information about the amount of inhibition occurring. We can assume that a high off/on sensitivity ratio, that is a lower threshold for the off- than for the on-effect ( $\text{off} > \text{on}$ ), reflects an increase in inhibition, although the relationship between the ratio and the amount of inhibition need not be a direct one. By studying both the  $R/B$  ratio and the off/on ratio and their relationship to one another, we should learn more about the part played by the cones in the responses of the cat retina and also to what extent they are concerned with inhibition.

#### METHOD

The large Wright colorimeter (Wright, 1946) was set for the two wave-lengths chosen ( $0.650\mu.$  and  $0.460\mu.$ ) and re-calibrated in terms of energy output; special attention was, of course, given to the removal of stray light.

The micro-electrode technique has already been described in detail (Granit, 1945, 1946, 1947). Decerebrate cats were used; these were given 4-6 c.c. of 10% urethane, intraperitoneally, to prevent head and eye movements.

Altogether 164 satisfactory elements were isolated in this series of experiments but, for various reasons, complete measurements were only made on 100. Each threshold, determined for both 'on' and 'off' and both for red and for blue, is based on an average of fifteen observations. The actual number of observations necessary to determine any given threshold was dependent on the amount of spontaneous activity present.

*The material.* Of the 164 elements, 16% were pure on-elements, 5% pure off-elements, and 79% on-off-elements. An element was not considered to be pure 'on' or pure 'off' unless its type of response remained the same when it was stimulated with a wave-length of 0.500  $\mu$ . (position of maximum sensitivity of visual purple) at the maximum intensity obtainable on the colorimeter.

Of the 100 elements whose responses were fully analysed, nineteen were pure on-elements, eight pure off-elements and seventy-two on-off-elements. The slight increase in the combined percentage of pure on- and pure off-elements simply reflects the greater chance of making a complete analysis where there are only two thresholds (those to red and blue) instead of four (red and blue to both on and off) to be determined.

It was decided that six on-off-elements, in which the threshold for the off-component was extremely high, and six in which the threshold for the on-component was correspondingly high (only to be elicited by maximum green stimulation in each case) could be added to the pure on- and pure off-groups respectively. Therefore, judged by this less exacting criterion, there were twenty-five pure on-elements, fourteen pure off-elements and sixty-one on-off-elements. Of the sixty-one on-off-elements the reactions of two were not completely measured because the colorimeter did not deliver a high enough red intensity to give the red on-effect.

A statistical analysis of all the results was made by Dr Leonard Goldberg (Karolinska Institutet). All the results are given in terms of sensitivity (reciprocal of the threshold) so that greater relative values of  $R$  or  $B$  mean greater relative sensitivities. We are not concerned with absolute sensitivities in the present investigation. An accuracy of 20% was possible in determining each threshold so that a 40% variation could be allowed within each of the groups into which the elements were divided. Most of the results were clear without statistical analysis.

## RESULTS

For all elements for which it could be obtained, the on-sensitivity to blue ( $B$ -on) was taken as the fundamental sensitivity and made equal to 100 in calculating the results. For those elements which showed no on-effect the off-sensitivity to blue ( $B$ -off) was used.

*On-elements:*  $R = B$  in 44% of these,  $R > B$  in 24%, and  $R < B$  in 32%. Thus, the majority of these elements show a pure visual purple response while a third are blue-sensitive and only a quarter red-sensitive.

*Off-elements:*  $R = B$  in 35.7%,  $R > B$  in 64.3% and none had  $R < B$ . Therefore in this group two-thirds of the elements are red-sensitive, one-third are governed by visual purple and none are blue-sensitive.

*On-off-elements:* The main group is divided into two sub-groups, so that the sensitivities of the on- and off-responses can be examined separately.

(a) On-components:  $R = B$  in 32.2%,  $R > B$  in 67.8% and there were no blue-sensitive components. Thus, as for the pure off-elements, two-thirds of these elements were red-sensitive at 'on' and one-third were dominated by visual purple.

(b) Off-components:  $R=B$  in 14.8%,  $R>B$  in 85.2% and there were no blue-sensitive elements. Thus, in this sub-group most of the elements were red-sensitive, a small proportion only being dominated by visual purple.

TABLE 1

On-elements <i>R</i> -on/ <i>B</i> -on	On-off-elements						Off-elements <i>R</i> -off/ <i>B</i> -off	
	Group I: on > off (average off/on ratio = 0.17)		Group II: on = off (average off/on ratio = 1.02)		Group III: on < off (average off/on ratio = 4.0)			
	On	Off	On	Off	On	Off		
<i>R</i> / <i>B</i> ratio	0.86	1.75	2.38	2.01	2.95	3.59	3.90	1.45

On account of the large range of variation the figures given for each group have been calculated from the logarithmic values.

The average values used in the figures and table are calculated from the logarithms of the actual figures. In the table the average *R*/*B* ratios for the three types (pure 'on', 'on-off' and pure 'off') of elements are given. For  $B=100$  the average value for *R* for pure on-elements is 86 (*R*/*B* ratio 0.86) and for pure off-elements 145 (*R*/*B* ratio 1.45). These values are statistically significant. There is, therefore, a slight dominance of blue-sensitivity in the population of pure on-elements and a more marked dominance of red-sensitivity in the population of pure off-elements. Only one *R*/*B* ratio in the latter group fell below 1.0 (it was 0.73) and the maximum value was 2.53.

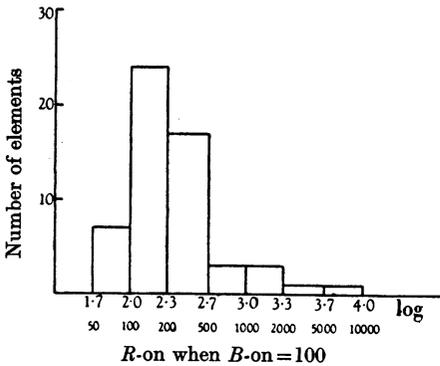


Fig. 2. Distribution of red-sensitivity for the on-components of on-off-elements.

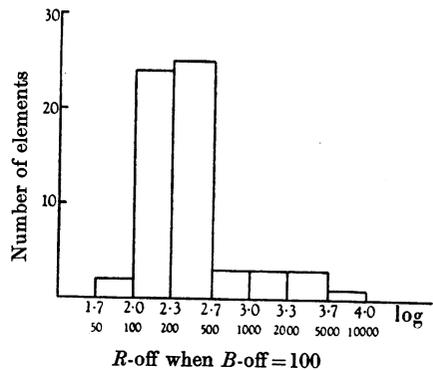


Fig. 3. Distribution of red-sensitivity for the off-components of on-off-elements.

For the on-off-elements the average values are of less interest on account of the wide individual variations ranging from  $R/B=1.0$  to  $R/B=50$ . The results are, therefore, best illustrated by the distribution curves given in Figs. 2 and 3. These show the number of elements exhibiting various amounts of red-sensitivity for both the on-response (Fig. 2) and the off-response (Fig. 3). It

will be seen that the really high  $R/B$  ratios are to be found among the on-off-elements.

However, the most striking point about the reactions of the on-off-elements is the enormous range of variation in the off/on ratio both for blue and for red. We shall come back to this point later.

If the on-off-elements are divided into three groups, according to whether off < on, off = on or off > on, then 47.9% of all the on-off-elements fall into the first group, 28.2% into the second and 23.9% into the third when the red wavelength was used as the stimulus. Almost the same percentages were obtained with blue. The majority of the on-off-elements are, therefore, more sensitive to the onset than to the cessation of illumination.

It can be seen from the table that there is a systematic increase in red-sensitivity as one passes from the pure on-elements by way of the off < on and off = on to the off > on of the on-off-elements. This means that, at least for the pure on- and on-off-elements, an increased sensitivity at 'off', which indicates an increased sensitivity to inhibition, is correlated with an increased sensitivity to red, and this indicates a more prominent cone reaction. It is true that the pure off-elements do not fit into this pattern since they show a lower  $R/B$  ratio than any of the on-off-elements. The table also shows that, within each of the three groups of on-off-elements, the  $R/B$  ratio, which can be used as a cone/rod index, is always higher for the off- than for the on-component.

*General comments.* Only on-off-elements were isolated in numbers large enough for further statistical analysis. We shall, therefore, summarize the results of a general comparison of the properties of the three types of element before going on to consider the reactions of the on-off-elements in more detail.

We have seen that in a population of pure on-elements the majority show either  $R = B$  or  $R < B$ . This means that the on-elements are largely dominated by rods. One would expect a retina containing a high proportion of rod-elements to have a fairly simple synaptic organization in which the on-response of the receptors, integrated by the bipolar and ganglion cells, would be more or less directly reflected in the discharges recorded from the nerve fibres. The guinea-pig has such a retina (Granit, 1945) in which most, although not all, of the elements show no off-effect. Histologically the guinea-pig retina contains rods only.

Further, the dominator curve of the guinea-pig eye is always the scotopic one (reflecting the dominating influence of visual purple) irrespective of the state of adaptation; there is no Purkinje shift (Granit, 1942). However, after light-adaptation the shape of the sensitivity curves indicated that some blue and green modulator elements were present and on a few very rare occasions there was evidence of red modulator elements as well. The blue modulator elements were quite easy to detect in this pure rod retina and this finding

becomes particularly interesting in view of the present indication of blue-sensitive receptors among the pure on-elements of the cat retina. We have here additional evidence in favour of the idea that the blue-sensitive end-organs of the retina are, in fact, rods (cf. Willmer, 1946). The reactions of both blue- and green-sensitive receptors might be due to photochemical substances produced by simple transformations of the visual purple molecule as a result of light-adaptation. There is also a possibility that the properties of those elements whose sensitivity to red is but little greater than that to blue are due to the presence of green- rather than red-sensitive receptors. The sensitivity curve of the green modulator unit extends farther towards the red end of the spectrum than that of the blue one and might, therefore, produce a final slight preponderance of red- over blue-sensitivity.

In general, one may say that the cone/rod indices ( $R/B$  ratios) found by us for the different types of element indicate cone activity in those elements which are subject to inhibition (show an off-effect). That this is not the whole story is shown by the fact that a third of the pure off-elements gave a pure rod response ( $R=B$ ) and a quarter of the pure on-elements gave a cone response ( $R>B$ ). In these cases we have rods associated with inhibition and cones free from inhibition (these may possibly be intermediate forms between the true rod and the true cone). The values of the  $R/B$  ratios given in the table suggest that the on-off-elements cannot be made up by the combination of a pure on- with a pure off-element. Rather must they represent various combinations of four types of receptor, inhibitory (off) cone, excitatory (on) cone, inhibitory (off) rod, and excitatory (on) rod. The fact that the on- and off-components of an on-off-element have different  $R/B$  ratios is impossible to understand if one assumes that, within a given element, a cone discharging down an inhibitory (off) path is identical with one discharging down an excitatory (on) path. However, the excitatory cones in one element might, as we shall see later, be inhibitory for *another* element.

The on-off-element seems to be the really important one in the cat retina, a retina which has, according to Walls (1942), 'a very respectable number of cones . . . about a third as many as we ourselves'. This type of element accounts for about 80% of the retinal units and of this number about 66%, if one judges by the behaviour of the on-component, or about 86%, if one judges by the behaviour of the off-component, contain cones. It is clear that the on-off-element must be the most important one not only for colour discrimination but also for other visual discriminations. For instance, the mechanism for appreciating contrast must be located in a retinal structure capable of responding both at 'on' and at 'off'.

The spectral sensitivity curve of the dark-adapted cat (Granit, 1945) shows too that cones must participate in the response to stimulation by yellow and red light. The average sensitivity to this part of the spectrum was too high to

be mediated by a pure visual purple mechanism and higher than was found in the guinea-pig. These particular measurements were all made on the on-effect irrespective of the type of element under investigation.

*Analysis of the on-off-elements.* The fact that the red- and blue-sensitivities may vary independently of one another shows that the two types of stimulus must often affect different structures within the same element. This, of course, is the basis of our idea that, provided the  $R/B$  ratio is greater than unity, the red-sensitivity affords a measure of the amount of cone activity, and therefore perhaps the number of cones, within the element in question.

The distribution curve of the off/on sensitivity ratio for red is given in Fig. 4. Although the extreme values are rare there is a wide variation in the values found for this relationship. We shall discuss the significance of this variation, which appears to be a fundamental property of the retina, later on.

In addition there is a close correlation between  $R$ -off and  $B$ -off (see Figs. 5 and 6). Individual elements may behave differently but, in general, a high sensitivity to red at 'off' is associated with a high sensitivity to blue at 'off' and vice versa. This suggests that the reactions of the red- and blue-sensitive receptors within the element are combined before they reach the ganglion cell, and are responsible for a common off/on ratio. In other words, the off/on ratio is determined at the synapses.

On the other hand, there is, as we have already seen, a tendency for the  $R/B$  ratio to increase with the off/on ratio (Fig. 7). When the  $R/B$  ratio is greater than unity, threshold stimulation with red light is actually a selective cone stimulation since the stimulus must be below the threshold of the other receptors. Since the  $R/B$  ratio tends to be higher for those elements which are exceptionally sensitive to 'off', we have yet another association between the presence of cones and an off-effect.

No definite correlation could be found between the red-sensitivity at 'on' and at 'off'. However, it is perhaps worth mentioning that when the values were arranged according to the red on-sensitivity and then divided into two equal groups, all the higher off-sensitivities to red were in the group which contained the  $R/B$  ratios of over 1.75 for 'on'. This means that the on-components of elements highly sensitive to 'off' tend to show cone activity too, but the absence of precise correlations between the on- and off-thresholds forbids the drawing of definite conclusions.

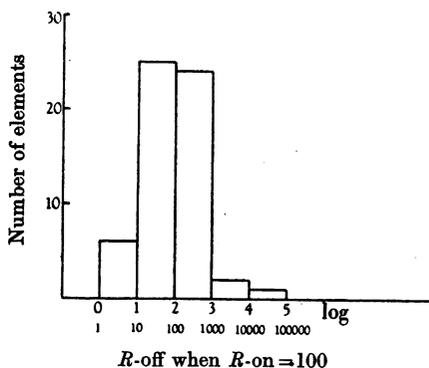


Fig. 4. Distribution of off/on ratio to red.

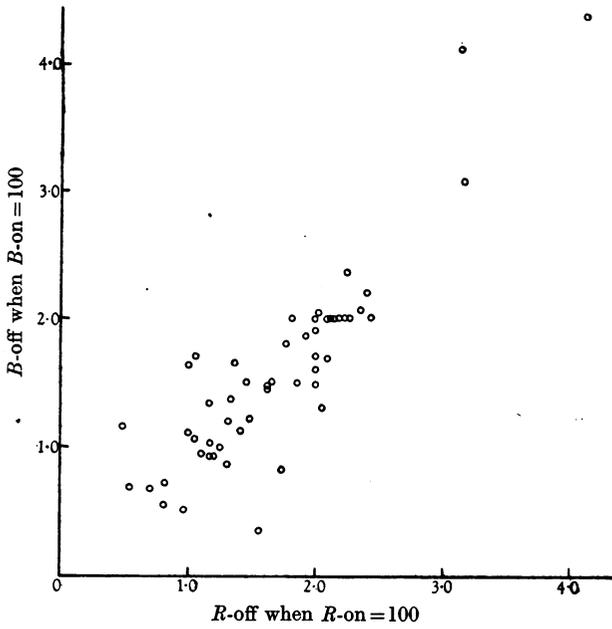


Fig. 5. Variation of the off/on ratio for blue with the off/on ratio for red (log. units).  
Regression coefficient =  $1.19 \pm 0.05$ . Correlation coefficient =  $0.96 \pm 0.01$ .

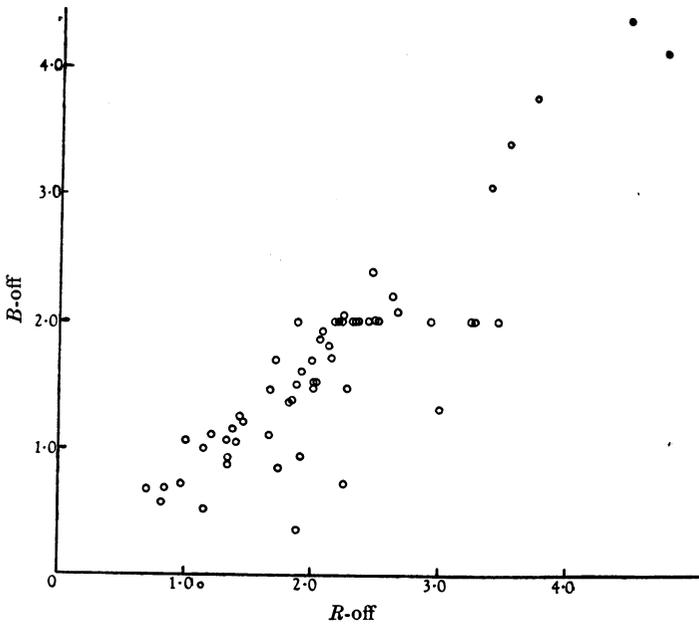


Fig. 6. Variation of  $R$ -off for  $B$ -off = 100 with the off/on ratio for blue (log. units).  
Regression coefficient =  $0.82 \pm 0.07$ . Correlation coefficient =  $0.83 \pm 0.04$ .

## CONCLUSIONS

The only retina so far investigated which is quite without synapses is that of the horseshoe crab, *Limulus*. It is only possible to record on-responses from this eye (Hartline & Graham, 1932) so that it is likely that off-responses do not appear unless the retina contains synaptic structures. If the cones of the cat's retina were themselves capable of responding to stimulation by off-effects one would expect to find a close correlation between the off/on ratio for red and the  $R/B$  ratio for the off-effect. Instead the dominant correlation is between the off-sensitivities to red and to blue. As we have seen, this can only mean that the off-effect arises in the synapses and that it does not much matter which trigger, rod or cone,

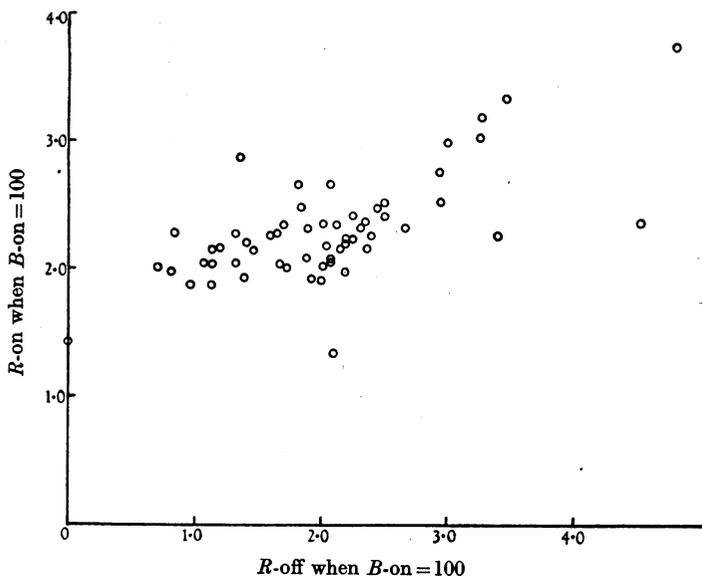


Fig. 7. Variation of the  $R/B$  ratio for the on-component with the off/on ratio (log. units).  
Regression coefficient =  $0.29 \pm 0.02$ . Correlation coefficient =  $0.93 \pm 0.02$ .

is touched off at the receptor level so long as the message passes through a cone synapse or is somehow affected by a mechanism usually associated with a cone response. At this point it should once more be emphasized that the use of threshold stimuli means that, where the  $R/B$  ratio is high, red stimulates cones only. Rods can only respond to a threshold red stimulus where  $R = B$  or  $R < B$ .

We can now formulate four criteria for the off-effect-inhibition system. It must be located between the receptors and the nerve fibre in the synaptic structures of the retina; it must in some way be closely connected with the cone synapses, but at the same time it must be possible for the rods to activate it; finally, it must have a design which can explain the wide variations found in the off/on ratio, variations which are quite outside the range to be expected from a relatively homogeneous biological system.

The straightforward synaptic connexions from the receptors to the ganglion cells by way of the bipolar cells do not fulfil these conditions very well. The differences between the rod and cone paths are not, so far as we know at present, great enough to explain why the  $R/B$  ratios for 'on' and 'off' in the same element are not identical. It is also difficult to see any reason for the variability of the off/on ratio.

Our four conditions are better satisfied if the horizontal cells, to which, indeed, Polyak (1941) has already attributed inhibitory properties, are included. He shows them as connecting pure cone pedicles to the vitreal ends of *both* rods and cones (Fig. 8). If we assume that an inhibitory block is produced at this particular spot, the discharge from both rods and cones would be blocked at the onset and released at the cessation of illumination. The inhibitory block would not originate in the element under the micro-electrode but in another neighbouring element. In this way the variability of the off/on ratio is readily accounted for, since the on- and off-responses are in fact quite unrelated having arisen in different retinal receptors. However, since the horizontal cells are only found in connexion with cones, one would expect a higher regression coefficient between cone activity (red-sensitivity) and off-sensitivity than we, in fact, found (Fig. 7). Further, there is no obvious way in which the rods could produce inhibition as they apparently sometimes do. This difficulty could perhaps be got over by assuming that some of the elements in which  $R=B$  do contain cones but in numbers too small to change the reaction to  $R>B$ . If this were the case the apparent inhibitory action of some rods would in fact be due to these cones. When one considers the large number of retinal elements which show off-effects and the small number of cones relative to rods in the cat retina, it is clear that cones must be extremely efficient inhibitors of the reactions of adjacent elements whether these are due to rods or cones. If cones were unable to inhibit the responses of adjacent cones it would be very difficult to explain how selective stimulation with threshold red could produce any off-effect at all.

However, inhibitory activity need not necessarily be restricted to the association paths of the horizontal cells. Unfortunately, we know far less about the amacrine cells. They are numerous, to be found in all parts of the retina and

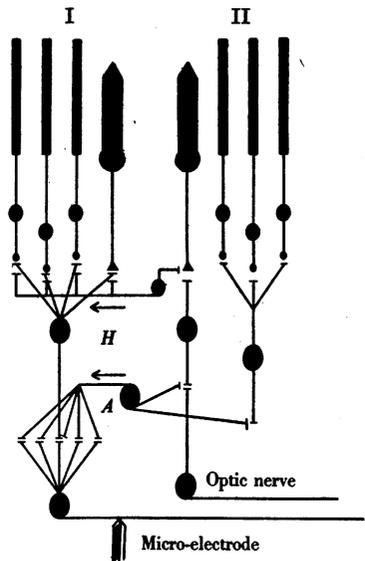


Fig. 8. Diagram of the retinal structure illustrating suggested inhibition pathways. *H*, horizontal cell path (Polyak); *A*, amacrine cell path.

form association paths rather higher than the horizontal cells. Reference to Fig. 8 will show that all our conditions would be satisfied if the amacrine cells, either alone or in combination with the horizontal cells, caused the inhibitory block which must precede an off-effect. In particular, the third condition, that rods as well as cones could set off the reaction, would be fulfilled since the amacrine paths connect the retinal elements *after* the rod and cone responses have reached a common path. The variability of the off/on ratio is even easier to account for on this view than if the horizontal cells are the agents of inhibition, since the higher the level the greater the likelihood of differences in the reactions of adjacent elements.

The fact that the  $R/B$  ratio can show such big variations, in spite of the small *absolute* number of cones present, shows that either the group of receptors connected to a nerve fibre to make up a retinal element containing a fair number of cones must be very big, or that its rods can be inhibited by its cones.

Finally let us consider the significance of the variability of the off/on ratio for vision. This is not merely a threshold variation, for we have measured the variation of impulse frequency with stimulus intensity for different colours in twenty-five isolated retinal elements and found great variation in the shapes of the intensity-frequency curves both for 'on' and for 'off'. The clue to the retinal mechanisms underlying discrimination must certainly lie in what, on the surface, merely looks like a bewildering variability. Every change of light, every slight shadow, every alteration in the visual field produced by minute eye movements must give rise to ever-changing on-off pulsations. The presence of elements of the three types on > off, on = off and on < off ensures that these fluctuations register every increase and decrease in illumination over a wide intensity range. This activity will, of course, be very marked at the points where the images of contours fall on the retina.

#### SUMMARY

1. The micro-electrode technique was applied to the analysis of the reactions of 100 isolated retinal elements in the dark-adapted cat. Equivalent stimulus values for the dark-adapted eye for a red ( $0.650\mu.$ ) and a blue ( $0.460\mu.$ ) wavelength were obtained by applying a correction factor based on the sensitivity of visual purple and the energy distribution of the colorimeter lamp. If, after this correction has been applied, threshold sensitivity to red is equal to that for blue ( $R = B$ ) then the reactions of the element in question must be dominated by visual purple. If  $R > B$  then red-sensitive receptors (cones) must determine the reactions and if  $R < B$  blue-sensitive receptors must be active in the element.

2. By measuring the  $R/B$  ratio for pure on- and pure off-elements, it has been possible to demonstrate that the pure on-elements are dominated by rods, and that cones are present in a great majority of both on-off-elements and pure off-elements. Blue-sensitivity was restricted to the pure on-elements.

3. The off/on ratio was measured for the on-off-elements. Since the occurrence of an off-effect is evidence of preceding inhibition the off/on ratio is a measure of inhibitory activity just as the  $R/B$  ratio is a measure of cone activity. It was found that the appearance of inhibition was associated with the presence of cones.

4. The results have made it possible to formulate four conditions which must be satisfied by any retinal structure postulated as responsible for the inhibitory system. These conditions are best satisfied by the amacrine cells possibly in combination with the horizontal cells.

5. The off/on ratio showed a variation of 1 to 100,000. The extent of this variation is considered to be of fundamental importance for visual discrimination. It must also be taken into account in any consideration of the localization of inhibition in the retina.

6. The  $R/B$  ratio for the on-off-elements varies from 1 to 50 despite the limited absolute number of cones, so that the retinal element must either contain a large number of receptors or the cones must be able to inhibit the rods within the same element.

A grant to the Nobel Institute for Neurophysiology from the Rockefeller Foundation is herewith gratefully acknowledged.

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