

NEURAL ORGANIZATION OF THE RETINAL ELEMENTS, AS REVEALED BY POLARIZATION

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THE CURIOUS OBSERVATION (2) that the on/off-elements, isolated by the micro-electrode technique in the cat's retina, formed two symmetrically organized structures responding similarly to the opposite poles of a polarizing current but in an opposite fashion to identical poles, was expanded by Gernandt and Granit (10) into an analysis of pure on- and pure off-elements and an attempt to correlate polarity and off/on-ratio at the threshold of illumination. In the present phase of our work polarization analysis and measurements of off/on-ratios are among the most important tools for penetrating further into questions concerning the functional organization of the retina.

DEFINITIONS, PROCEDURE AND PROBLEMS

The definition of the polarity of a retinal element requires a fixed position of the electrodes used for polarization. The system of reference is illustrated in Figure 1. The preparation is a fully dark-adapted decerebrate cat. Its left eye is used. The polarization electrodes—silver silverchloride wires—are alongside the bulb in the nasal and temporal corners of the eye. Since the micro-electrode forms an obtuse angle with the shaft fixed to the micromanipulator, the retinal elements can be picked up only in the nasal half of the field. The commutator is used for making the nasal electrode anode or cathode during stimulation.

One of the lines of current is drawn in the diagram of Figure 1. But it should be clearly realized that the stimulating currents penetrate a volume conductor. Hence the retina may be stimulated by lines of current traversing the elements in different directions. A schematic view of the possibilities involved may be obtained by imagining a number of laterally expanding lines of current rotated 360° around their horizontal axis between the two poles.

Definitions. A cathodal element responds to the make of the cathode (nasal electrode) by an on-response, to the break of it by inhibition. To the make of the anode the cathodal element responds with inhibition, to the break of it by excitation as an off-discharge. An anodal element has opposite properties. It responds to the make of the threshold anodal current by an on-discharge, to the break of it by inhibition. To the make of the cathodal current the anodal element responds by inhibition, to the break of it by an excitation off-discharge.

Hence an element is defined as anodal or cathodal with respect to the nasal electrode (at which the micro-electrode is situated) according to whether the *on-discharge* at the "make" is elicited by the anode or by the cathode. The other effects can then be predicted by the rules set forth above. The definitions refer to threshold effects of the polarizing

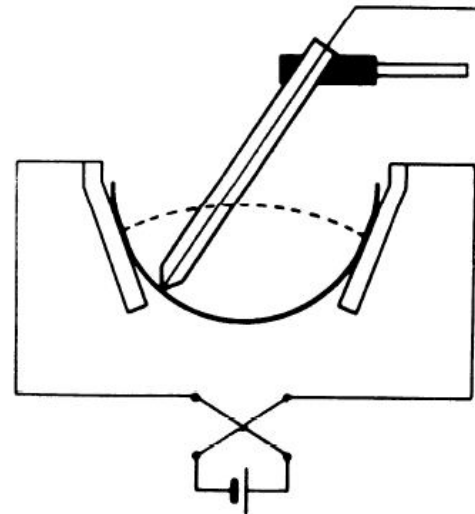


FIG. 1. Diagram demonstrating micro-electrode inserted in retina, polarization electrodes with battery and commutator. A resistance of 50.000 Ω in series with the retina and ammeter not included.

currents. Some of the on/off-elements do not show a definite polarity. Depending upon the position of the micro-electrode, threshold effects can be elicited from about 0.05 mA upwards. I have but rarely used elements with thresholds above 1.0 mA. Since one of the main variables has been current strength in terms of multiples of rheobasic effects, it has been necessary to select low-threshold elements in order to have a large range of current strengths available for the experiment. This is because too strong currents disturb the signal/noise ratio of the amplifiers.

Pure on- and pure off-elements respond with pure on- or off-effects to illumination with wave-length 0.520μ of our large Wright colorimeter (11), when tested with stimuli from threshold to full strength. The on/off-elements respond, *at least within part of this range*, with both on- and off-discharges, *i.e.*, they respond to both onset and cessation of illumination. In the most sensitive animals the colorimeter allows a range of stimulus strength of 3-5 logarithmic units. Unit intensity is the threshold intensity. This extreme sensitivity to the feeble stimuli delivered by a spectrum can only be obtained with fully dark-adapted cats which need not be anaesthetized but can be used in the decerebrate state. A few cc. of urethane (20%) intraperitoneally serves to suppress eye movements. It is best to give the animal at least one full hour of dark adaptation and not less than two hours to settle down after the ether narcosis at the operation. Only large spikes, 0.15-0.30 mV, have been used because these have been shown by Gernandt (7) to be of identical appearance and also because smaller spikes cannot be maintained long enough. A couple of hours is often required by the experimental problem. All thresholds have been determined by listening to the discharge but photographs have been taken to illustrate characteristic phenomena.

The problems. In the course of extensive experiments both Gernandt and I have independently and as a matter of routine measured the polarities of pure on-, pure off- and on/off-elements in order to check up on the conclusions which were based on a smaller material (10). The main problem, however, has concerned the effect of anodal and cathodal poles on the light threshold of elements of different type. The experiments were begun by determining type and polarity of the element isolated. Then the thresholds for illumination and for polarization were measured. Finally the light thresholds were measured *during* polarization with currents of varying strength. The unit current strength is the rheobase. Polarization currents are given in multiples of the rheobase. Similarly threshold changes during polarization are given in multiples of the normal light thresholds before polarization.

RESULTS

Polarity and type of element. Gernandt and Granit (10) found all the pure on-elements to be cathodal. Both of us, in the course of work on various problems, have since determined the polarities of a large number of pure on-elements. Neither of us has seen any exception to this rule.

We had previously found all the pure off-elements to be of opposite polarity, *i.e.*, anodal. From this rule Gernandt (8) has never seen any exceptions but, in the course of my work, I have found two cathodal pure off-elements. It is difficult to know whether these two exceptions were apparent or real. The on-component of an on/off-element is a great deal more sensitive to disturbing factors such as local or general asphyxia, pressure by the micro-electrode, etc., than the off-component. It is possible that the two exceptions were damaged on/off-elements which had lost their on-component.

According to Gernandt (8), the dark-adapted on/off-elements, for which the off/on-ratio at the threshold has been determined with wave-length 0.520μ of the spectrum, can be cathodal or anodal for practically any off/on-ratio but, in general, anodal elements tend to have high off/on-ratios, cathodal elements low off/on-ratios. This means that inasmuch as the on/off-elements approach the pure on- or the pure off-type they tend to become cathodal or

anodal, similar in this respect to the pure types. But it is to be noted that state of adaptation (complete dark adaptation) and wave-length (0.520μ) enter into this statement (8). The two polarities are symmetrically distributed if the off/on-ratios are measured with red lights (8).

Simultaneous records of anodal and cathodal elements. Occasionally it is possible to apply a micro-electrode in such a fashion that it records from two adjacent elements. One element is then just below it and accordingly produces a large spike; the other one, less well localized, produces a smaller spike. An example is shown in Figure 2. The large spike has a faster spon-

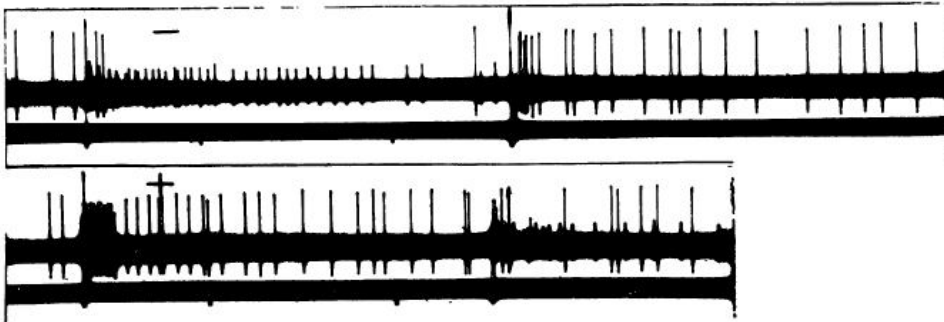


FIG. 2. A large and a small spike isolated by the same micro-electrode. Stimulation between the two clearly visible shock artefacts with nasal electrode cathode (above) and anode (below). One second marked on lower line in the middle of each period of stimulation. Note opposite responses of small and large spike during and after polarization. All records to be read from left to right.

taneous rhythm. In the upper picture the small *cathodal* spike is stimulated by the cathode, whereas the large *anodal* spike is inhibited during polarization and accelerated into an off-discharge at the break of the current. In the lower picture the poles have been reversed. The large anodal spike is seen to be excited by the anodal current, and its spontaneous activity is somewhat suppressed afterwards. The small cathodal spike, however, is accelerated at the break into a brisk off-discharge, demonstrating that it had been inhibited during polarization. Such systems are always more or less symmetrical, as pointed out above (see Definitions). Stimulus strength was low, 0.5 mA, corresponding to 5 rheobases.

The same preparation is used in Figure 3. From above downwards strength of illumination is increased in an experiment with wave-length 0.460μ . The uppermost record is just above the threshold. There is a third still smaller spike, difficult to follow. The two main ones are the same ones as in Figure 2. The large anodal spike has a very much lower threshold to illumination. Already at relative intensity 0.012 it responds with both on- and off-discharges. When strength of stimulus increases, the off-discharge of the large spike gradually increases in frequency but the on-component is inhibited. It is interesting to see that the inhibition of the large spike *during illumination* corresponds to excitation for the small spike. In the lowermost record there is complete inhibition of the large spike by illumination but a

great acceleration of the small spike. At cessation of illumination only the large spike responds. There was possibly a small off-effect in the small spike at the low intensity, marked 0.047, but at the maximal intensity none is visible.

Comparison with Figure 2 shows that the transition in Figure 3 from a low- to a high-intensity response to illumination looks like the change from anodal to cathodal electrical stimulation. It is, of course, possible to regard

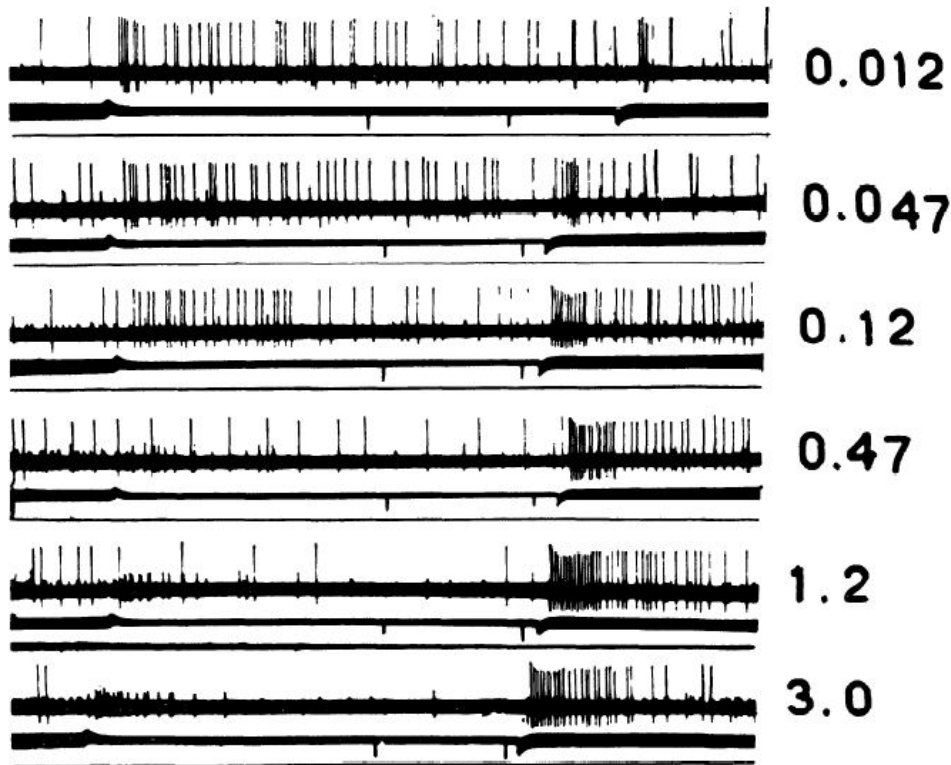


FIG. 3. The large and small spike of Fig. 2 elicited by illumination with wave-length 0.460μ at the relative intensities indicated beside the records. Period of illumination marked by photocell and amplifier connected to second beam of cathode ray below the one recorded from. This beam also records the 50-period A.C. of the mains but, at this film speed, so compressed that the duration of 1 second has been indicated by separate marks below it. Same principle adopted in all the figures to follow.

this remarkable correspondence between effects of illumination and polarization as something fortuitous but other experiments (see below) show that polarity really means something. The presence of opposite slow potentials in the retina also adds significance to the fact that some on/off-elements are anodal, others cathodal. The elements of opposite polarity seem to be part and parcel of a system organized for a definite purpose. Cathodal and anodal electrical stimuli can be used to switch that system into operation. We have tried to devise experiments utilizing this electric "switch" to enhance or suppress the anodal or cathodal components of an element in order to find out what happens to its sensitivity to light and whether by such experiments any information can be obtained about the functional organization of the elements.

Effect of current strength. Working with stimuli from selected parts of the spectrum Gernandt (6) noted that polarization with a constant current of 1.0 mA often caused large and selective fluctuations in the light thresholds of on/off- and pure off-elements whereas the light thresholds of the pure on-elements were but little influenced by the current. This indicated some fundamental difference of design in the different types of element. The light thresholds of some on/off-elements were also relatively indifferent to polarization. For this reason a systematic analysis of the effect of current strength on the light threshold for a stimulus of wave-length 0.520μ was held to be desirable. The rheobasic strength of the polarizing current was determined in every case and the light threshold measured before and during polarization with currents of different strengths in terms of rheobasic multiples.

The general effect of an increase of current strength as such is illus-

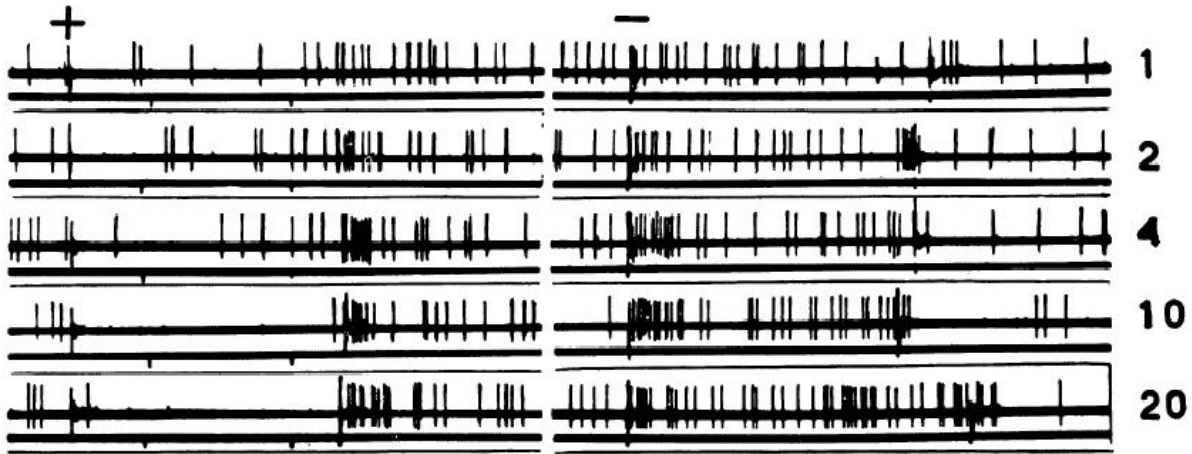


FIG. 4. The effect of currents of opposite direction on cathodal element. Increasing current strength (right) in terms of multiples of rheobase (uppermost record). Onset and cessation of electrical stimulation clearly shown by shock artefacts.

trated in Figure 4 for a cathodal on/off-element at 1, 2, 4, 10 and 20 rheobases. To the left (anodal stimulation) is seen the increasing inhibition succeeded by its off-effect, to the right (cathodal stimulation) the increasing excitation succeeded by the postexcitatory inhibition of the spontaneous rhythm. An anodal element would have behaved in an opposite fashion to the same currents. The simple and typical relations of Figure 4 are often broken down for strong polarizing currents from 5 rheobases upwards. When this happens, a phase of excitation initiates what otherwise would have been a pure inhibitory effect. An example is found in the brief phase of excitation for cathodal stimulation at 20 rheobases in Figure 4. The postexcitatory inhibition of the spontaneous activity is preceded by a brief off-discharge at the break of the current. We need not discuss these complications, mentioned in a previous paper (2). It suffices to remember the general rule that during polarization cathodal elements are excited by cathodes and inhibited by anodes—anodal elements *vice versa*.

Current strength and light thresholds. Considering that the general background excitability of an element can be altered in the direction of facilitation or inhibition by the polarizing current (Fig. 4), one is entitled to expect the changes in the light thresholds during polarization, which actually were demonstrated by Gernandt (6). His work, restricted to polarization with a constant current of 1.0 mA, had shown that the light thresholds of pure off- and of on/off-elements often were quite sensitive to polarization whereas those of pure on-elements were far more stable. These questions were now re-investigated with currents exceeding the rheobasic strength by known amounts.

Currents of up to 60 times the rheobase were used in the analysis of a considerable number of low threshold *pure on-elements*. These being cathodal, the facilitation occurred during cathodal polarization but it never succeeded in diminishing the light threshold (*i.e.*, increasing the sensitivity) by more than thrice its original value. An effect of that order was rare. Generally the effect was very much smaller or altogether lacking. The effect on the light threshold of the opposite pole, the anodal inhibition, was practically non-existent—a singular fact when compared with the exceedingly high sensitivity of the light threshold to inhibition during polarization of certain on/off-elements (see below). One of the really fundamental distinctions between retinal elements is their differentiation into elements which *cannot* (pure on-elements) and elements which *can* give an off-effect (3, 5). With respect to polarization, the pure off-elements behaved like the anodal on/off-elements and need not therefore be discussed separately.

In the following simple experiment with an on/off-element a fact of great theoretical significance would seem to be involved. A cathodal on/off-element with an off/on-ratio of 0.17 was analysed at 30 rheobases of polarization strength. There was no effect whatever on the light threshold of the on-component during cathodal polarization; for the off-component the facilitation was 5.8 (times the original value). However, current reversal caused an anodal depression of the light threshold of the on-component of 146, whereas the light threshold of the off-component remained uninfluenced at 1.0. This is a good instance of what might be called the *specificity of the connexions* involved. The effects at different poles, though in a general way symmetrical with respect to the discharge set up or blocked by the current (see Fig. 2), are often extremely asymmetrical when measured in terms of the sensitivity to light during polarization. Other examples of this general asymmetry will be found below. If an off-less or an on-discharge to light is facilitated by one pole, it need not therefore be inhibited by the opposite pole or *vice versa*. The connexions, whether excitatory or inhibitory, are, or *can* be, specific ones for specific purposes.

The light thresholds of the anodal on/off-elements were, practically without exception, easily inhibitable by cathodal polarization, which, as pointed out above (see Definitions), inhibits at the make. As a rule the off-effect was a great deal more inhibitable than the on-effect. Occasionally the light

thresholds were equally inhibitable for onset and cessation of illumination. A typical case is illustrated in Figure 5. It is one of the many anodal elements with the interesting property that the impulse frequency to onset of illumination increases over a limited range of increasing light intensities and then again decreases. The large spike of Figure 2 shows this effect of illumination. Record 1 of Figure 5 is the normal control, at 78 times the light threshold for the on-component, at 16 times the threshold for the off-component. (In multiples of light threshold strength the intensities differ for "on" and "off" because of the off/on-ratio.) Record 2 of Figure 5 shows that cathodal polarization at 20 rheobases has slightly decreased the number and frequency of the impulses at onset of illumination but completely extinguished the off-

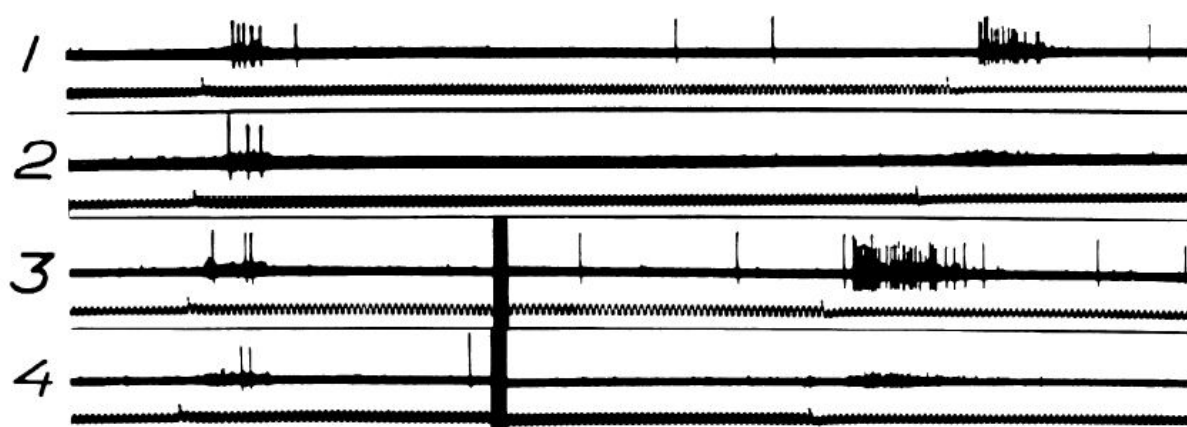


FIG. 5. Anodal element. 1, normal response to illumination; 2, same during cathodal stimulation; 3 and 4, similar pairs but for 10 times stronger illumination, as fully explained in text. About 1 second cut out in the middle of records 3 and 4.

component. Next follows, in record 3, a normal control after a ten-fold increase of illumination strength. In record 4 illumination at this strength is repeated during cathodal polarization. There is very little change at onset, but complete inhibition of the discharge at cessation of illumination. The inhibitory pathways, activated by cathodal polarization, were thus, in this case, particularly well developed for the illumination off-component. Sometimes they blocked the on- and off-components almost symmetrically.

Cathodal on/off-elements were a less homogeneous group with respect to the depressing effect of polarizing currents on the light threshold. The majority of them behaved like the similarly cathodal pure on-elements. Their light thresholds were thus practically insensitive to anodal inhibition. Also with respect to facilitation these elements often behaved like the pure on-elements. There was, however, another considerably smaller group of cathodal on/off-elements in which both inhibition and facilitation were of almost the same order as in the anodal on/off-elements.

Curves for inhibition and facilitation. The quantitative aspects of the inhibition of the light threshold during polarization provided some interesting features, illustrated in Figure 6 for the off-component of an anodal on/off-

element and for a pure off-element. The light threshold is measured during cathodal polarization. There is an initial modest increase of the depression up to about 3–8 rheobases; then suddenly, as if some new structure of higher threshold had been stimulated by the current, every further increase of cur-

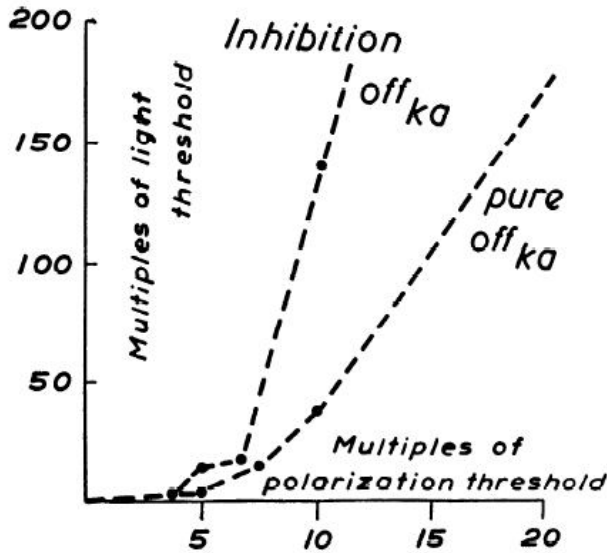
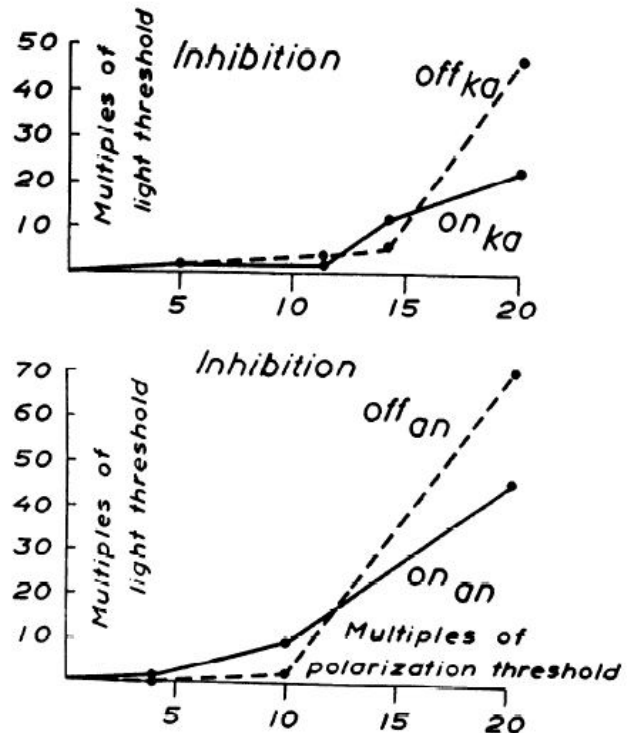


FIG. 6. Plot of increase of light threshold (inhibition) for wave-length 0.520μ against polarization strength for the off-component of an anodal on/off-element and for a pure off-element, both polarized cathodally. Full explanation in text.

FIG. 7. Same as in Fig. 6 for an anodal (upper) and a cathodal (lower curves) element but the elements polarized with currents of opposite direction. Both on- and off-components recorded.

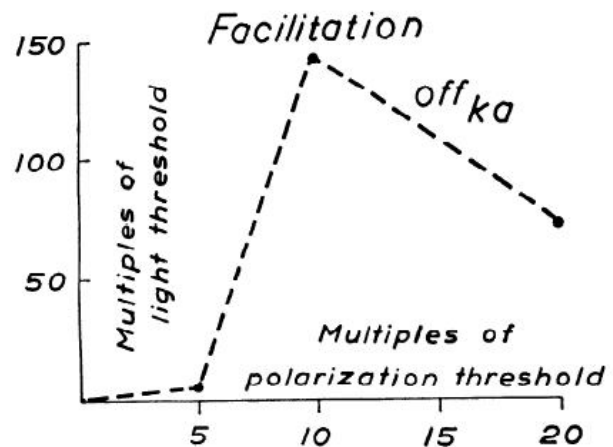


rent strength produces a large increase of the inhibition. This second phase of the curve is lacking in the cathodal pure on-elements and in the majority of the cathodal on/off-elements. But, when a cathodal on/off-element is inhibitable, then it too possesses the second phase of the curve. Figure 7 compares an anodal on/off-element with a cathodal on/off-element in which

the depressions during polarization were of the same order. Both the on- and the off-components were inhibited. There is less inhibition of the on-component. As a rule the off-component is more sensitive to inhibition than the on-component. Sometimes their sensitivity is of the same order. In one cathodal on/off-element (mentioned above) the on-component was selectively inhibitable.

Facilitation during polarization with the pole that determines the character of the element (whether anodal or cathodal) is a more irregular affair. If facilitation were determined by an effect of the polarizing current upon the receptors themselves, it is difficult to see how it ever could be anything

FIG. 8. Same as in Fig. 6 but this time decrease of threshold (facilitation) for the off-component of a cathodal on/off-element during cathodal polarization.



but exceedingly modest. In measurements of absolute thresholds in a fully dark-adapted eye the receptors are already giving their very best performance. There is little scope for facilitation. A real difficulty in measurements of facilitation is also that in some elements the stimulating current sets up such a high frequency of discharge that the acceleration necessary for the threshold, if at all present, cannot be distinguished in the loudspeaker.

Figure 8 is an example of the enormous facilitation which sometimes—though rarely—can be obtained. It shows a cathodal on/off-element with an off/on-ratio as low as 0.008, thus an extremely high-threshold off-component. At the optimum of facilitation for the off-component around 10 rheobases the off/on-ratio rose to about 1, because the on-component did not at all “feel” the current. Such large facilitations are found in cases in which the off/on-ratio is very much off the mean value, located slightly to the “on”-side of equality. A somewhat similar case is illustrated by the records of Figure 9. This was an element in which an off-component was on the verge of turning up, and sometimes did so, but never quite established itself. Record 1, at 100 times the illumination threshold, illustrates this doubtful off-effect which just as well could be an after-discharge and not a real increase at “off.” Record 2, during anodal stimulation at 10 rheobases, might have been a normal record. But the last record 3, taken during cathodal stimulation, shows a definite off-discharge preceded by inhibition during illumination.

At "on" there is a slight increase of the frequency which in this cathodal element was accelerated by the cathode, as can be seen by comparing with the frequencies before illumination. The illumination off-discharge was regularly facilitated by cathodal stimulation.



FIG. 9. Cathodal element. All records show effect of illumination at 100 times the light threshold (wave-length 0.520μ). 1, normal control showing uncertain off-effect; 2, illumination during anodal; 3, illumination during cathodal polarization. See text.

CONCLUSIONS AND DISCUSSION

We may regard it a well established fact that what is called a retinal element is in most cases an exceedingly complex structure (3, 5, 9). The effect of the electrical current need not necessarily be direct; it can also be indirect, over internuncial neurones. The simplest element is the pure on-element that almost certainly reproduces the behaviour of receptors directly converging towards the common end-station. This element (in cats and guinea pigs) is by several criteria a rod element (3, 5). The different spectral sensitivity of the on- and off-component of an on/off-element (9), as well as the enormous range of variation of the off/on-ratio (5, 10), demonstrates that in on/off-elements widely different receptors have been joined together, partly or even largely over internuncials, to form a structure intended for specific tasks in vision, one of which certainly is to provide a basis for contrast.

1. The pure on-element reflecting the behaviour of the receptors responds to the current in a simple fashion. It is excited by the cathode, and if after current reversal the strength of it be increased, it also discharges an anodal off-effect. There is very modest facilitation and practically no inhibition of the light threshold when the retina is illuminated during cathodal or anodal stimulation respectively. From this it is concluded that in the on-element *the structures responsible for large facilitations and inhibitions are missing. Accordingly, the receptors themselves cannot have been the structures giving those effects on the light threshold.*

It is perhaps permissible, on the basis of this evidence, to suggest that the pure ascending convergence path to the nerve is cathodal. It should

further be noted that the absence of an off-effect in the pure on-element establishes the fact that its electrical anodal off-effect has no physiological counterpart in its response to illumination. The physiological off-effect of the pure off-element is possibly identical with its electrical off-effect that is cathodal. There again the anodal on-effect has no counterpart in its response to illumination.

2. The on/off-elements are provided with special structures for facilitation and inhibition of the light threshold. These structures may be highly specific, sometimes inhibiting or facilitating both the on- and off-component of the response to illumination, sometimes either component alone. Reversal of polarity does not necessarily turn a facilitation into an inhibition or *vice versa*. Accordingly, the specific connexions, activated by the current, may also be described as structures determining the off/on-ratio.

3. Since the absolute light threshold of the fully dark-adapted eye is being measured during polarization, large facilitations can never occur in the receptors themselves which are maximally sensitized. They must always be due to internuncials removing an inhibition normal for the element in question. The absence of inhibition of the light threshold in the pure on-element likewise proves that the large inhibitory effects arrive over internuncials. The light thresholds of several on/off-elements are also insensitive to polarization, demonstrating again that specific structures are required for this purpose. A path over receptors, bipolars and ganglion cells does not suffice.

4. These inhibitions and facilitations of the light threshold do not represent abnormal states but organized effects in the cone system. This conclusion is based on the fact described in a separate paper (4), that measurements with spectral stimuli during electrical facilitation and inhibition reproduce the modulators of the cat's eye and never the visual purple distribution of sensitivity. The electrical stimuli therefore inhibit or facilitate through the mediation of structures normally engaged in modifying the primary response of the receptors over internuncial channels. Where these particular internuncials are missing, as in the pure on-element, very little happens.

5. From the fact that in on/off-elements the threshold currents for inhibition and facilitation of the light stimulus exceed the rheobasic currents by 4-10 times or more, it is concluded that the specific facilitating and inhibiting associational structures either are orientated in another (less accessible) fashion than receptors and bipolars or else are relatively few or of high threshold (fine calibre?) compared with them.

6. The light thresholds of anodal elements are especially sensitive to inhibition by cathodal stimulation, particularly at "off." There *may* be elements which possess a true on-sensitivity to anodal stimulation (2) but we *know* that the simple on-element and several on/off-elements are cathodal. Hence a large number of elements surrounding the one recorded from must always be cathodally stimulated. Inasmuch as they send inhibitory internuncials to the element selected (*e.g.*, in the manner suggested by Brooks and Eccles, 1), there will be inhibition. The anodal character of an element

suggests that indirect effects over internuncials play a large part in its design.

7. A large number of cathodal on/off-elements—in my experience the majority of them—respond to currents of rising strength like the similarly cathodal pure on-elements. Their light thresholds are relatively independent of polarization. Such elements may therefore be structurally akin to the pure on-elements and contain a large number of rods. Their electrical off-effect is anodal but this need not give any information about their off-response to light.

8. Theoretical difficulties are provided by the small group of cathodal on/off-elements in which the light thresholds are almost as sensitive to polarization as those of the anodal group. The difficulty consists in the fact that the effects on the light thresholds are of opposite polarity compared with those of the anodal group. Why this complete reversal of polarity? Are there specific anodally and cathodally sensitive structures (2), or are the inhibiting and facilitating structures in these elements of opposite orientation? It is clear that an orientation theory can always be adjusted to explain all the facts, particularly in a structure where there is evidence for indirect excitation and inhibition (3, 5), but how about the possibility of anodally and cathodally sensitive cells? The best argument in favour of the latter view would seem to be the fact that, if there be *large* facilitations and inhibitions of the light threshold, then the direction of these effects (with a few exceptions generally confined to relatively weak currents) depends upon the polarity of the element concerned. The polarity of an element, a definition which states at which pole an element is excited by the make of the current (depression being elicited by the opposite pole), therefore tells us something fundamental about its organization and nearly always predicts the polarity of facilitation and inhibition over internuncials. The chief objection to accepting the idea of specific anodal and cathodal receptors is that the well-established concept of indirect excitation and inhibition offers too many possibilities for solving this problem along other lines (5, 10).

SUMMARY

With reference to a pair of electrodes in the nasal and temporal corners of the eye, the fully dark-adapted retinal elements of the cat are "anodal" or "cathodal," that is, stimulated either by the make of the anode or the make of the cathode and depressed by the opposite pole. Depressions are succeeded by off-effects at the break of the current.

Simultaneous records of adjacent anodal and cathodal on/off-elements show that depression of the one may coincide with excitation of the other (Fig. 2).

The light thresholds of pure on-elements, studied with currents from rheobasic strength to 60 times the rheobase, do not change very much under the influence of the electrical currents.

The light thresholds of the anodal on/off-elements can easily be suppressed by cathodal polarization, particularly at "off."

Most cathodal on/off-elements behave like the pure on-elements. Their light thresholds are relatively insensitive to polarization. A smaller group behaves like the anodal on/off-elements but with reversed polarity.

Sometimes very great facilitations of the light threshold can be obtained in on/off-elements.

The large inhibitions and facilitations are initiated by specific structures, often independent for the on- and off-component of an on/off-element, but their polarity is determined by the polarity of the element.

From these facts a number of fundamental conclusions (see final section of paper) can be drawn about the neural organization of the retinal elements.

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REFERENCES

1. BROOKS, C. McC. and ECCLES, J. C. An electrical hypothesis of central inhibition. *Nature*, 1947, 159: 760-764.
2. GRANIT, R. The distribution of excitation and inhibition in single fibre responses from a polarized retina. *J. Physiol.*, 1946, 105: 45-53.
3. GRANIT, R. *Sensory mechanisms of the retina*. London, Oxford University Press, 1947, xxiii, 412 pp.
4. GRANIT, R. The mammalian colour modulators. *J. Neurophysiol.*, 1948, 11: 253-259.
5. GRANIT, R. AND TANSLEY, K. Rods, cones and the localizations of pre-excitatory inhibition in the mammalian retina. *J. Physiol.*, 1948, 107: 54-66.
6. GERNANDT, B. Colour sensitivity, contrast and polarity of the retinal elements. *J. Neurophysiol.*, 1947, 10: 303-308.
7. GERNANDT, B. The form variations of the spike recorded by a micro-electrode applied onto the mammalian retina. *Acta physiol. scand.*, 1948, 15: 88-92.
8. GERNANDT, B. Polarity of dark adapted on/off-elements as a function of wavelength. *Acta physiol. scand.*, 1948. (In course of publication.)
9. GERNANDT, B. (Work in course of publication.)
10. GERNANDT, B. AND GRANIT, R. Single fibre analysis of inhibition and the polarity of the retinal elements. *J. Neurophysiol.*, 1947, 10: 295-302.
11. WRIGHT, W. D. *Researches in normal and defective colour vision*. Kimball, London, 1946.