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CHANGE OF ORGANIZATION IN THE RECEPTIVE FIELDS OF THE CAT'S RETINA DURING DARK ADAPTATION

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When the amount of light entering the eye is reduced its performance is modified. One aspect of this is the reduction of resolving power which has been measured in man in psychophysical experiments (Koenig, 1897, 1903; Broca, 1901; Hecht, 1928; Pirenne & Denton, 1952). Another aspect is the increased amount of area summation that occurs at low intensities (Lythgoe, 1940; Craik & Vernon, 1941; Barlow, 1957). These changes in performance might result, in part at least, from changes in the nervous pathways in the retina. We therefore planned to examine the effect of the level of illumination on the spatial distribution of sensitivity in the receptive fields of the large type of ganglion cell (Rushton, 1949) isolated in the cat's retina with micro-electrodes of the kind used by Granit & Svaetichin (1939).

The receptive field of a retinal unit is the area of the retina from which responses can be elicited by light, but the borders are not accurately defined because the area is extended if the intensity of the light used to test for a response is increased (Hartline, 1940; Kuffler, 1953; Barlow, 1953). Kuffler also showed that, if the intensity of the test spot is kept constant, the intensity of the background has an effect; the receptive fields expand if this is decreased and shrink if this is raised. The size of the receptive fields thus appears to depend on the *relative* intensity of test spot to background light. In contrast, the changes in psychophysical performance referred to seem to depend on the *absolute* intensity of light entering the eye; for instance, one of us has shown that lowering the intensity of an adapting background field increases the amount of spatial summation that occurs when test stimuli are superimposed upon it (Barlow, 1957). We therefore set out to compare the sizes of the receptive fields and their organization in light-adapted retinæ and in retinæ which had dark-adapted to a steady threshold. As reported elsewhere (Barlow, FitzHugh & Kuffler, 1957), this may take three hours, and many of the

preparations used in the dark-adaptation experiments were also used in the present investigation.

In the light-adapted cat Kuffler (1953) has shown that the receptive fields are often arranged so that the central region and the annular surrounding zone are mutually antagonistic, and evoke discharges at the opposite phase of a light stimulus. Thus, in an 'on-centre' unit, light falling in the centre of the receptive fields causes a discharge at 'on', and usually inhibits at 'off'; light falling in the surround usually inhibits at 'on' and excites at 'off'. In the experiments described here we found that removing the background light and allowing dark adaptation simplified the organization. The characteristic effects of stimulating the surround during light adaptation dropped out, so that the receptive fields appeared smaller, and gave the same discharge throughout their extent. This change might be thought to conflict with the increased spatial summation found in the psychophysical experiments, but this is not so, because the peripheral zone of the receptive field which is lost after dark adaptation does not augment discharges evoked from the centre, but rather tends to inhibit them.

METHODS

A complete description of the apparatus, preparation and calibrations has been published by Talbot & Kuffler (1952), Kuffler, FitzHugh & Barlow (1957) and Barlow *et al.* (1957). Ether-decerebrate cats with III, IV, V and VI nerves divided were used, since these gave stable preparations in which it was possible to hold single units for several hours through the time required for dark adaptation. Single units were isolated in the intact eye by 10–15 μ micro-electrodes placed on the vitreal surface of the retina, and action potentials were displayed and recorded with conventional electrophysiological apparatus, and an impulse interval meter (MacNichol & Jacob, 1955). The multibeam ophthalmoscope required a minor addition which enabled a light stimulus to be distributed in an annular zone surrounding the central region of the receptive fields. This consisted of a glass plate with a central opaque spot which could be placed in the same position as the range of holes of different sizes; these were all in a plane parfocal with the retina.

Thresholds were defined as the weakest stimulus intensity which caused a perceptible change in the maintained discharge (which was constantly present in healthy preparations; Kuffler *et al.* 1957) of the units in at least 50% of trials, the 'perceptible change' being judged by the experimenter. Whenever possible repeat determinations of threshold were made, and if a series of thresholds was being measured, the repeat series was done in reverse order.

RESULTS

The changed effect of peripheral stimulations after dark adaptation

The first method of investigation was to determine the threshold of the preparation to spots of different sizes, all concentric, and centred as closely as possible on the centre of the receptive field. This has previously been used to show summation within the receptive field and inhibition from the surround in single units of the frog's retina (Barlow, 1953), and it was hoped that it would give useful information about the over-all pattern of organization and distribution of sensitivity within the receptive fields in the dark- and light-adapted state.

Fig. 1 shows the results of such an experiment on an off-centre unit. First the unit was dark-adapted to a steady threshold, which took 90 min. Then the threshold for the range of spot sizes was measured using a 7 msec flash (curve c); as the spot size increased the threshold fell with a slope almost that predicted by Ricco's Law of area summation (product of stimulus intensity and illuminated area is constant for constant response—broken line in figure). Although the curve flattened out appreciably for the larger areas, there was still some drop in threshold out to a spot diameter of 1.5 mm (6.7°). This procedure was repeated with the longer flash duration of 380 msec, but this curve (d) showed no drop in threshold beyond 1 mm (4.4°) diameter, and in

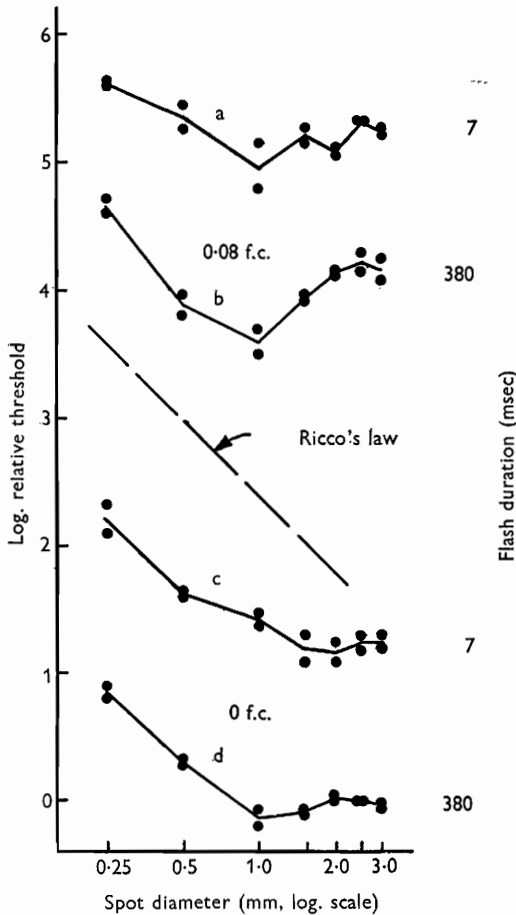


Fig. 1. Change of threshold intensity for off-centre unit as diameter of the white stimulating spot is changed, using two different flash durations as indicated. Curves a, b were made with a blue-green background which gave a retinal illumination of 0.08 f.c.; curves c, d, with no background. Broken line has the slope predicted by Ricco's Law of area summation.

fact there is a hint that the threshold rose slightly when the more peripheral parts of the receptive field were included. Subsequently a blue-green background light of 0.08 f.c. was shone on the retina, and after allowing a few minutes for light adaptation, curve 'a' was obtained with 7 msec flash duration, and curve 'b' with 380 msec duration. These curves show considerable summation up to 1 mm (4.4°) spot diameter, but thereafter the threshold intensity rose as the spot size was increased. The rise was small in the case of the brief stimulus, whereas it was pronounced for long duration stimuli. When the background intensity was raised still further to 45 f.c., the curve for the long duration flash (not shown here) rose even more steeply when the peripheral region of the receptive field was included. These results were typical of several ganglion cells, and occurred with on-centre as well as off-centre units.

The interpretation of the increase in threshold intensity which occurs when the stimulus spot exceeds a certain size is, presumably, the same here as for the similar curves obtained on 'on-off' units in the frog's retina (Barlow, 1953); the outlying regions antagonize the central region, and the threshold therefore rises when these are included. It is already known (Kuffler, 1953) that such antagonism exists in the light-adapted cat's retina, so curve 'b' was as predicted. With zero background there was little change in threshold as the spot diameter was increased above 1 mm (curve d), which suggests that this antagonism does not occur in the dark-adapted retina. Moreover, the diameter of the whole receptive field appears to be smaller in the dark- than in the light-adapted state. Finally, curves 'a' and 'c' show that this antagonism fails to develop as fully with brief flashes as with longer ones.

In the experiment of Fig. 1 the stimulus intensity was varied so as to keep the response constant, i.e. threshold. Instead, the stimulus intensity may be kept constant, and the varying response to different sizes of stimulus observed. For instance, if a small spot (0.1–0.2 mm diameter) was centred on the receptive field of a dark-adapted off-centre unit, it produced, at an intensity near threshold, a decrease in the discharge frequency during the flash and a small off burst following it. These effects, the suppression of the maintained discharge and the off burst, increased with increasing spot diameters up to about 1 mm, but a further increase in diameter made no additional changes to the response. If the experiment was done on a light-adapted unit, the threshold intensity for the smallest spot was greater, as expected, but the responses were similar to those in the dark-adapted units up to spot diameters of about 0.5 mm. With larger spot diameters the response was significantly and consistently different. Instead of suppressing the maintained discharge, the flash (in a typical off-centre unit) actually increased the activity; this was attributed to the 'on' discharge elicited from the periphery of the receptive field. The off burst following the flash was also diminished as the inhibitory action of the

periphery at 'off' revealed itself. Such an experiment confirms that the antagonism of centre and surround exists only in light-adapted retinal units. In dark-adapted units, stimuli of moderate intensity only elicit the response characteristic of the centre.

Reversal of discharge

A spectacular demonstration of this change in organization of the receptive field is obtained by using a stimulus light which falls near the edge of the dark-adapted receptive field. In the dark-adapted state this stimulus elicits a discharge at the same phase of illumination as one falling on the centre—at 'on' in an on-centre unit and at 'off' in an off-centre unit. Upon light adaptation a similarly placed stimulus may produce the opposite effects, giving 'off' discharges and inhibition at 'on' in an on-centre unit, and 'on' discharges with inhibition at 'off' in an off-centre unit; furthermore, these responses may occur when the stimulus intensity, though stronger than that required in the dark, is not much higher than that required to excite the centre of the light-adapted receptive field.

This kind of result appears to show that some parts of the receptive field actually reverse their contribution to the ganglion cell upon light adaptation, but our observations are not exact enough to prove that this is really so. For reasons given in the discussion we suspect that the regions which give the reversed contribution after light adaptation lie outside the dark-adapted receptive field; if this is correct, the type of result described above would occur when the stimulus spreads over regions lying both inside and outside the dark-adapted receptive field.

Duplicity theory and the change in organization

It was natural to suppose that the change in the action of the peripheral zone of the receptive field during dark adaptation was associated with rods taking over from cones. Thus it might be suggested that the cones are connected to the ganglion cell in such a way that those at the periphery of the receptive fields inhibit the actions of those at the centre, causing 'off' discharges if the latter cause 'on' discharges, and vice versa, whereas rods are only connected like the central cones. Some evidence against such a hypothesis can be obtained from the dark-adaptation curves of Figs. 2 and 3. Thus in Fig. 2 curves (a) and (b) show the progressive drop in threshold to a blue-green (a) and a red-orange (b) central stimulus spot. Between 50 and 80 min the blue-green threshold was dropping much faster than the red-orange because, according to the duplicity theory, rods were taking over from cones, and rods are less sensitive to red-orange light relative to blue-green light than are cones. On looking at the lower set of curves for which annular stimuli of the two colours were used, it will be seen that the rapid drop in blue-green

threshold occurs at the same time; there is a period from 80 to 120 min during which the annulus gave 'off' responses in this on-centre unit, yet during this period the relative thresholds to red-orange and blue-green light show that the rods, not the cones, caused the response. This obviously contradicts the hypothesis that the mutual antagonism of the centre and surround is characteristic of the connexions made by cones exclusively, and this is borne out by examination of Fig. 3. Looking at the top pair of curves, for central stimulation, the relative values of the threshold to red-orange and blue-green stimuli

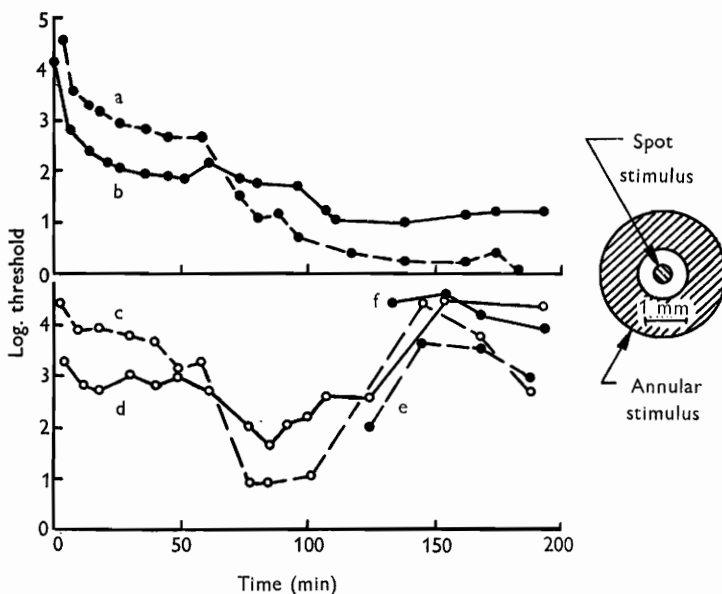


Fig. 2. Thresholds of an on-centre unit to flashes of blue-green (Wratten 75), ---, and red (Wratten 29), —, light during dark adaptation; flash duration 380 msec. Stimulus lights are focused on the hatched areas in the inset diagram. Curves a, b, made with 0.5 mm diam. spot; curves c, d, e, f, with annulus of internal diam. 1.25 mm: ●, thresholds for 'on' responses; ○, thresholds for 'off' responses. Previous light adaptation, 25 min at 40 f.c. retinal illumination (uncorrected for losses in the eye).

show that cones were mainly responsible for the discharge early in light adaptation, and the rods took over between 10 and 30 min from the start. The same is true of the bottom pair of curves, which show the thresholds to a stimulus spot covering the whole of the receptive field, but the switch from cones to rods occurred somewhat earlier. The central pair of curves show the threshold for eliciting an 'off' response in this on-centre unit by stimulating the whole of the receptive field, and it will be seen that the threshold for blue-green light was lower, indicating that the antagonistic type of response was dominated by rods, even early in dark adaptation. We are uncertain why the rods took over from the cones at different times in different parts of the receptive

field, but it is possible that the light adaptation was less strong in the periphery.

The experiments of Figs. 2 and 3 establish that the change in organization of the receptive field need not occur at the same time as the change from cones to rods; these experiments contain additional information which will be considered later in connexion with the time of occurrence of the change in

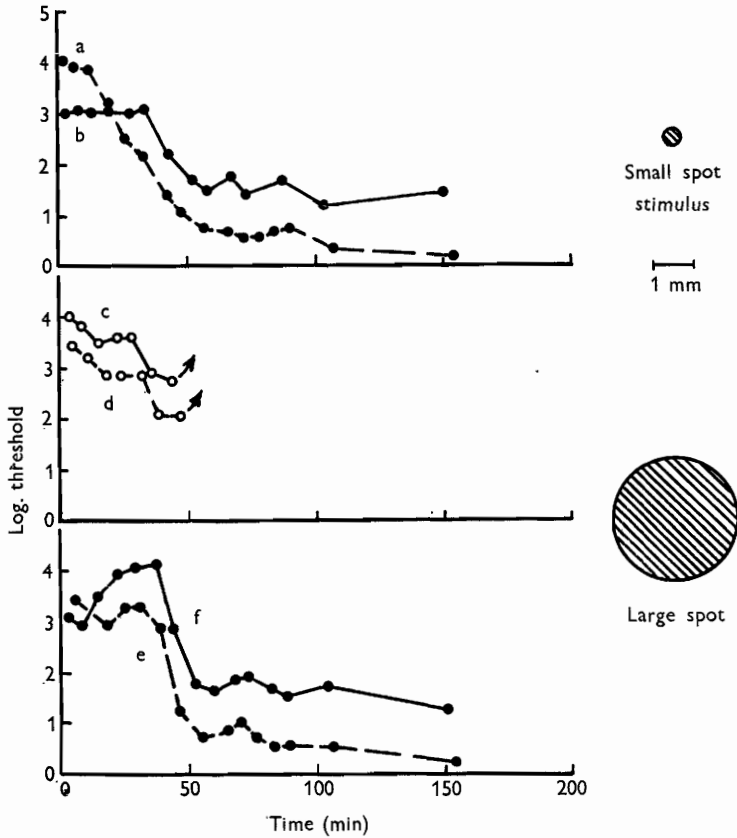


Fig. 3. Thresholds of an on-centre unit to flashes of blue-green (curves a, d, e) and red (curves b, c, f) light during dark adaptation; flash duration 380 msec. Curves a, b, made with 0.5 mm diam. stimulus spot; curves c, d, e, f, with 3.0 mm diam. spot; conventions as Fig. 2. Previous light adaptation, 80 min at 5 f.c. retinal illumination.

organization. The fact that the organization of the receptive field is not simply dependent on the type of receptor which is active is indicated by another experiment which will be considered next.

The principle of this experiment was to determine area-threshold curves of the type shown in Fig. 1 using blue-green and red-orange light in the hope that these would stimulate rods and cones respectively, and thus show up the over-

all pattern of connexions made by them. The results are shown in Fig. 4. The top pair of curves (a and b) were obtained against a background intensity of 4.2 f.c., and both show the rising tail indicating inhibition from the outlying parts of the receptive field. The bottom pair was done after complete dark adaptation, and they both show the flat tail. It will also be seen that the Purkinje shift had occurred, for the threshold to red-orange light is lower for the top pair, whereas the blue-green threshold is lower for the pair done against zero background after dark adaptation. It would be possible to argue that the blue-green stimulus as well as the red-orange stimulus excited cones in the light-adapted state, and likewise that both colours excited only rods in the dark-adapted state; the top pair and the bottom pair of curves are

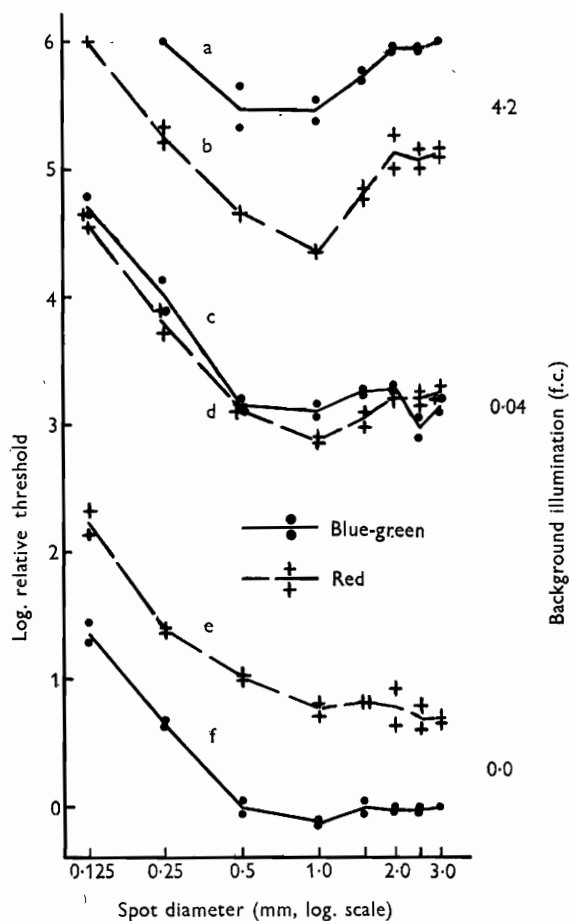


Fig. 4. Area-threshold curves for an off-centre unit made with a white background light (retinal illuminations listed on the right), and with blue-green and red stimulus lights, showing that lateral inhibition does not depend on the colour of the stimulus. Flash duration 380 msec.

therefore still consistent with the hypothesis that the change in organization of the receptive field is due to the change in the type of receptor which is active. For the middle pair of curves the intensity of the background was adjusted so that the curves for blue-green and red-orange stimuli occupied positions *relative to each other* which were intermediate between that of the top pair and that of the bottom pair. The Purkinje shift was therefore half complete, and under these conditions there can be little doubt that the blue-green stimulus, superimposed on the white background, will add to the excitation of rods principally, and the red-orange to the excitation of cones principally, yet the area threshold curves are only slightly different.

One other experiment of this kind was successfully completed, giving a similar result. Taking these together with the results of dark adaptation experiments of the type shown in Figs. 2 and 3, one can say with reasonable certainty that the different organization of the receptive field found in dark- and light-adapted retinae does not depend upon a difference in the connexions made by rods and cones.

Time of occurrence of the change in organization

Fig. 2 has been considered up to the point at which rods take over from cones, as indicated by the blue-green threshold suddenly dropping much further than the red-orange threshold. This change was complete by 80 min. A further change took place at about 120 min when the 'off' threshold to the annulus rose, and at about the same moment it became possible (for the first time) to elicit 'on' responses with the annular stimulus (curves 'e' and 'f'). The rise in threshold for the 'off' response with the annular stimulus presumably results from the dropping out of the antagonistic response in the periphery, which was the explanation offered for the results of the area-threshold experiments. The appearance of the 'on' discharge on annular stimulation might result from scattered light falling on the central zone, or from the annular stimulus actually overlapping this zone. Reference to Fig. 5 may make it easier to follow our suggested explanation for these changes.

The changes shown in Fig. 3 can be explained in the same way. Rods had taken over from cones by 30 min, and at about 50 min the antagonistic discharge of the periphery disappeared. 'Off' responses could then no longer be obtained by stimulating with the large stimulus spot. Between 40 and 50 min there was a large drop in on-threshold which presumably resulted from the cessation of inhibition at 'on' from the annular zone.

In both the above experiments the change in organization only occurred after the preparation had been in the dark for a long time. It would, however, be incorrect to suppose that the change always took as long as this to develop. It was sometimes noticed that the organization was changed almost as soon as one could test for it after putting the preparation in the dark. This seemed

to be the case when the preparation had not been strongly light-adapted, and the dark adaptation was consequently rapid. Such observations on the time of the change were incidental rather than systematic, but they seem to show that the antagonistic action of the peripheral zone of the light-adapted receptive field drops out rather abruptly at a moment near the end of dark adaptation.

DISCUSSION

The first point to be discussed is the nature of the changes in retinal organization during dark adaptation that the present results establish, and their relation to previous electrophysiological work. Secondly, there are some comments to be made about the possible mechanisms mediating these changes. The third point is the extent to which the changes found provide answers to the psychophysical problems which instigated this work. Lastly, the results lead to some speculations about the relation between receptive field organization and simultaneous contrast. The discussion is therefore divided into these four sections.

Nature of the change in organization

When we were doing these experiments we used to refer to the change that occurs upon dark adaptation as the 'reversal' in contribution of the peripheral zone of the receptive field. A patch of light which gives an 'on' discharge in a light-adapted off-centre unit may give an 'off' discharge after dark adaptation, and this is perhaps the most dramatic way in which the change reveals itself. The area threshold curves, however, show up the change in a more quantitative manner, and a careful inspection of them shows that to speak of it as a 'reversal' is rather misleading. In both Figs. 1 and 4, and in other similar experiments, the inhibitory action of the annular region surrounding the centre is shown by the rise in threshold when this is included in the stimulus by enlarging the spot from, say, 1 to 2 mm diameter. Now this pronounced inhibition in the light-adapted condition results from the inclusion of a region which causes, at most, only a slight change in threshold after complete dark adaptation. It may therefore be more accurate to speak of the change brought about by light adaptation as a growth of the antagonistic response from the region surrounding the dark-adapted receptive field, rather than as a 'reversal' of the response from this region. This explanation fits in with the changes of threshold during dark adaptation for stimulation with a small central spot, a large spot, and an annulus (Figs. 2, 3), and it can also be applied to the results of Donner & Wilmer (1950) who studied the discharge from single units in the cat's retina when the intensity of the stimulus was varied; their stimulus covered the whole of the receptive field, and they found a simplified type of discharge at low intensities which could be attributed to the discharge

characteristic of the surround dropping out when their stimuli were very weak.

Fig. 5 is a diagram showing how we think the receptive field of an on-centre unit is organized in the light- and dark-adapted states. On the left is the field from which 'on' discharges can be elicited in the dark-adapted state; upon light adaptation a surrounding region from which 'off' responses appear is added, as shown to the right. The edge then gives 'off' discharges, an intermediate zone gives 'on' and 'off', and a central region gives only 'on' discharges. Thus the receptive field actually seems to be larger in light adaptation than in dark adaptation, but instead of being simple with all regions yielding the same response, it becomes complex with mutually antagonistic regions giving opposing responses, as described by Kuffler (1953). It should be pointed out that in several respects this diagram goes beyond what is firmly established: for example, the outer limits to the receptive fields are based on area threshold curves rather than direct exploration, and it is uncertain how much the 'off' zone that is present after light adaptation overlaps the central 'on' region.

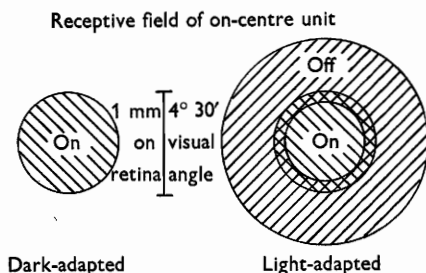


Fig. 5. Suggested organization of the receptive field of an on-centre unit in the dark- and light-adapted states. 'On' or 'off' responses to a long flash are obtained when the stimulus falls in the correspondingly labelled regions of the field. The positions of the limits to these regions have been inferred from area-threshold curves and have not been determined directly.

The difference between the dark- and light-adapted area-threshold curves of these units in the cat's retina is remarkably similar to the difference between curves obtained from 'off' and 'on-off' units in the frog's retina (Barlow, 1953). Complete dark adaptation may take at least as long in the frog as it does in the cat, so that a change of discharge type on dark-adapting might easily have been missed. Hartline (1938) evidently thought that the discharge produced by a ganglion cell was a fixed characteristic of that cell, but the present results suggest that this may also have to be reconsidered.

The comparison with the frog is interesting in another way. In the cat, if light falling in a particular part of the receptive field excites a discharge at 'on', inhibition will often occur at 'off'. This could show up by the reduction of the maintained discharge, by the reduction of a discharge evoked by stimulation elsewhere in the receptive field, or by the raising of the threshold

to excitation elsewhere in the receptive field. Similarly, if inhibition occurs at 'on', excitation will often occur at 'off'. The arrangement is different in the frog, for here both 'on' and 'off' discharges can be obtained from the centre of the receptive field, and the surrounding region, which may inhibit both types of discharge, is often incapable of evoking any discharge at all. The common feature of the arrangements in cat and frog is that parts of the retina laterally displaced from a part under consideration have an inhibitory action on discharge evoked from that part. In the cat this works both ways: the peripheral annular zone, which is laterally displaced from the centre, antagonizes or inhibits a discharge evoked from it; and the centre, which is laterally displaced from the surrounding regions, also inhibits discharges evoked from these regions. In the frog one can only show the inhibitory action of surround on centre, because the surround evokes no discharge. In both cases it is true that if light falls on the surrounding retina together with a particular central region, then the discharge expected from this region is diminished. *Lateral inhibition* therefore seems to be an appropriate term to use, though in grouping together these phenomena (and perhaps also the inhibitory action of adjacent ommatidia in *Limulus* shown by Hartline, 1949, and Hartline, Wagner & Ratcliff, 1956) one must bear in mind that there are species differences.

Mechanism of lateral inhibition

It might conceivably be possible to identify the structures responsible for lateral inhibition, and it is therefore worth while listing the properties of this pathway, drawing a contrast between it and the 'direct' pathway which, it is assumed, is followed by the activity resulting from stimulation of the centre of the receptive field.

- (a) It must conduct laterally up to at least 1 mm.
- (b) In the cat the pathway often has a 'two-way' action; if an increase in the light falling in the annular zone inhibits the discharge of the ganglion cell, a decrease in the light will excite, and if an increase excites, a decrease will inhibit. A pathway can only have such a 'two-way action' if it carries a maintained discharge which can be either increased or decreased, but it is of course possible that there are separate pathways conveying inhibitory and excitatory effects from the surround.
- (c) Our experiments showed that lateral inhibition could occur when rods alone, or cones alone, were active; therefore the pathway connects with both, probably in the same way as the direct pathway.
- (d) The pathway is not active after prolonged dark-adaptation; it then appears to have a higher 'threshold' than the direct pathway.
- (e) The inhibition does not show up if excitatory and inhibitory regions are excited synchronously with brief flashes; possibly it has a greater latency

or summation time than the direct pathway. This fact, together with (b) and (d) above, would be explained if the pathway took a long time to build up its full activity (slow recruitment), and if it had a very prolonged after-discharge—that is if it had the properties Sherrington described as ‘inertia’ and ‘momentum’.

Cajal’s (1894) and Polyak’s (1941) work shows that there is a bewildering variety of structures which might possibly mediate lateral inhibition, but this list of properties can at least be used to eliminate some of them. For example, lateral inhibition might result from receptors inhibiting their neighbours, but it is most unlikely that axons from receptors extend as far as 1 mm laterally. Another hypothesis, which fits many of the requirements, is that lateral inhibition results from the inhibitory action of recurrent collaterals from neighbouring ganglion cells (if they are present in the cat’s retina); this fails to account for the change of organization on dark-adapting, for the discharge of ganglion cells (at least of the type here isolated) is not greatly changed by the absolute level of illumination, so that the action of inhibitory collaterals should also remain unchanged. It is naturally tempting to pick on the horizontal or amacrine cells, since they appear to conduct laterally and have not had any other function assigned to them, but there are many varieties of bipolar cell, and the evidence is insufficient to decide between such possibilities.

Psychophysical aspects

Psychophysical experiments led to the expectation of a change in retinal organization in dark adaptation. To what extent do the changes described conform to these expectations? The first set of relevant data are those showing a change of acuity with level of illumination (see, for example, Koenig, 1897; Broca, 1901; Hecht, 1928; Pirenne & Denton, 1952). The slight decrease in the size of the central, summing, region of the receptive field that is shown in Figs. 1 and 4, and illustrated diagrammatically in Fig. 5, does not seem nearly big enough to account for the whole of the improvement in acuity which occurs when the amount of light entering the eye is increased. It is in any case difficult to believe that units with a receptive field covering almost 5° of the visual field are responsible for the optimum acuity of a cat’s vision at high intensities; it seems likely that there are smaller units which come in at higher intensities, as Pirenne & Denton (1952) suggested. Nevertheless, the lateral inhibition which develops at higher intensities may be one of the mechanisms which enable full use to be made of the information contained in the light absorbed in the retina; it seems admirably suited to preserve information about small differences in illumination between neighbouring regions of the visual field, and this is just the task which Rose (1948) claimed that the visual mechanisms could perform almost to the limit set by the quantal fluctuations in the light absorbed.

An increase in the area of a test stimulus results in a bigger drop in the threshold intensity in a dark-adapted eye than in a light-adapted eye (Lythgoe, 1940; Craik & Vernon, 1941; Barlow, 1957). This led to the idea that the retinal summation area was bigger in dark adaptation, which was attributed to increased interconnexion between receptors (Broca, 1901; Lythgoe, 1940), but the present experiments show that in these retinal units in the cat the most pronounced change on dark-adapting is the disappearance of lateral inhibition. Broca and Lythgoe correctly foresaw a change in retinal organization, but their suggestion appears to be doubly wrong in detail; there is a decrease, not an increase, in the amount of retinal interconnexion at low intensities, and the interconnexion which diminishes is of an inhibitory, not an excitatory, type.

Lateral inhibition and simultaneous contrast

Johannes Müller believed that simultaneous contrast was caused by the reciprocal action of adjacent retinal areas, and this view was strongly upheld by Hering in opposition to Helmholtz's explanation in psychological terms (see Rivers, 1900). The following explanation of brightness contrast seems to vindicate Müller and Hering, but there is not yet any evidence for a similar mechanism for mediating colour contrast.

The subjectively experienced degree of 'whiteness' or 'blackness' of a part of the visual field depends not only on the intensity of illumination of that particular part, but also on whether it is more or less intensely illuminated than the neighbouring regions. Similarly, the intensity of discharge in a particular unit depends not only on the intensity of light falling in the central region of its receptive field, but also on the intensity falling in the annular surrounding zone. It is natural to suggest that these two facts are related, and that lateral inhibition is the mechanism which mediates simultaneous contrast, but this would involve two further assumptions. The first is that a raised impulse frequency in an 'on-centre' fibre gives rise to the sensation of 'whiteness', and in an 'off-centre' fibre to the sensation of 'blackness'; possibly a decreased frequency causes the opposite sensations, but this is not necessary to the argument. The second assumption is that these sensations are referred to a point in the visual field corresponding to the central region of the receptive field, and are not referred to the annular surrounding zone even if the physical stimulus which gave rise to the impulses affected the surround. Thus if the intensity of illumination of the whole of a region of the visual field except for a small dot is suddenly increased, then one knows that extra impulses will arise in an off-centre unit which is centred on the dot; the corresponding experience is the sensation of blackness, which is, of course, referred to the region of the dot, though it results from stimulation of the surrounding parts of the retina.

This explanation seems to hold together, and there are two corollaries. The first is that simultaneous contrast should be reduced at very low intensities since lateral inhibition does not occur after complete dark adaptation. The second is that simultaneous contrast should be reduced when brief exposures are used, since lateral inhibition is less pronounced under these conditions. Both these predictions seem open to experimental testing. There is, however, no need to suppose that it is the only mechanism mediating simultaneous contrast, and Asher's (1953) experiments on binocular fusion suggest that there is also a central mechanism.

SUMMARY

1. The change of organization of the receptive field which occurs during dark adaptation has been studied in single units isolated in the intact eye of the decerebrate cat.

2. The least intensity that disturbs the resting discharge has been determined for stimulation by a range of concentric light spots of varying diameter centred on the receptive field of the isolated unit, and of 0.38 sec duration. Log. threshold intensities plotted against log. areas give area-threshold curves which show the over-all distribution of sensitivity in the receptive fields.

3. In the dark-adapted state the threshold decreases as the spot size is increased up to about 1 mm diameter; there is little change in threshold intensity when the spot size is further increased.

4. In the light-adapted state the threshold decreases as the spot size is increased up to about 1 mm diameter as in dark adaptation, but further increase of spot size up to about 2 mm diameter causes a marked increase of threshold intensity. The rise of threshold is attributed to the inhibitory action of the annular zone surrounding a ganglion cell, and it is concluded that this inhibitory action disappears after dark adaptation.

5. Area-threshold curves obtained with stimuli of 7 msec duration show less rise in threshold at large spot diameters.

6. In the dark-adapted state pure 'on' and 'off' units are found; these give discharges only at 'on' or only at 'off', and inhibition of the resting discharge at the opposite phase of the stimulus, wherever they are stimulated in their receptive fields. Upon light adaptation the opposite type of discharge can be elicited from an annular zone surrounding the dark-adapted receptive field, so that the units acquire a duplex character; 'on' units become 'on-centre with off-surround'; 'off' units become 'off-centre with on-surround'. The surround which produces the opposite type of discharge is responsible for the inhibition shown up in the area-threshold curves.

7. The change in organization occurs when dark adaptation is nearly complete; it is not simultaneous with the Purkinje shift.

8. Area-threshold curves obtained with red and blue coloured stimuli run roughly parallel to each other when done under photopic conditions against

a strong background, when done under scotopic conditions with no background, and when both rods and cones are active at intermediate intensities of background.

9. It is concluded that the different organization of dark- and light-adapted receptive fields does not result from different connexions made by rods and cones.

10. The relation between these findings and previous work on vision is discussed, and it is suggested that simultaneous contrast effects may result from the inhibitory action of laterally displaced parts of the retina, and that the increased area summation after dark adaptation may result from the disappearance of such lateral inhibition.

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