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RECEPTIVE FIELDS OF FROG RETINAL GANGLION CELLS: RESPONSE FORMATION AND LIGHT-DARK-ADAPTATION

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SUMMARY

1. The excitatory and inhibitory receptive field mechanisms of retinal ganglion cells were studied by extracellular recording from the eyecup of *Rana temporaria* in order to elucidate the nature of adaptational changes in the functioning of the receptive field.

2. The responses to large stimuli were always strongly depressed relative to responses evoked by smaller spots. This was true even in the fully dark-adapted state and at the very lowest stimulus intensities, showing the inhibitory surround to be effective in all states of adaptation and at all stimulus intensities.

3. Threshold measurements confirmed earlier findings, usually revealing the surround only in light-adapted states. However, in more than 10% of fully dark-adapted cells thresholds to large stimuli were significantly elevated.

4. The central summation area of the receptive field was found to shrink with light-adaptation. There was a gradual decrease in diameters, amounting to some 20–30%, from the dark-adapted, rod-determined receptive fields to the cone-determined ones.

5. Adaptation by bleaching and adaptation by backgrounds changed the effects of the surround in different ways. After a rhodopsin bleach the transition from a light-adapted to a dark-adapted situation was seen as an abrupt drop of large-stimulus thresholds at some time during adaptation. Steady backgrounds produced no such dramatic changes, but the increment threshold lines were somewhat steeper with test spots stimulating the surround than with smaller spots.

6. Although the discharge patterns generally show the strength of the surround influence, they underwent no qualitative change at the time of the drop of large-stimulus thresholds after a bleach.

7. It is suggested that the drop does not reflect a sudden reorganization of the receptive field, but is the consequence of the different ways the responses to large stimuli are formed in different ranges of stimulus intensity (pre-inhibitory at high intensities, post-inhibitory at low intensities), and of gradual changes in signal dynamics.

INTRODUCTION

In centre-surround organized receptive fields of ganglion cells in cat (Barlow, Fitzhugh & Kuffler, 1957) and frog (Donner & Reuter, 1965) threshold measurements clearly show the influence of the surround in the light-adapted eye, but fail to show it in the dark-adapted eye. Barlow *et al.* interpreted this as a change of organization

in the receptive field, meaning that the antagonistic surround is weak or absent in the dark-adapted eye. The interpretation has been questioned by other workers using post-stimulus time histograms as an index of the centre-surround balance (Enroth-Cugell & Lennie, 1975). Then little change could be seen in the effectiveness of the receptive field surround. This paper describes experiments that characterize adaptational changes in the response properties of frog ganglion cells. It is shown that the suppressive surround is not erased by dark-adaptation.

METHODS

The experiments were done on the excised and opened eyes of common frogs (*Rana temporaria* L.) caught in the autumn in Southern Finland and stored in basins at 4 °C. Before the experiments the frogs were kept for at least 12 h in the dark at room temperature. The eyes (diam. 5·5–7·0 mm) were dissected in dim red light and placed in a cooled chamber (10–12 °C except where otherwise stated). They were allowed to adapt to darkness for at least 1 h before the experiment began. Action potentials were recorded extracellularly with glass micropipette electrodes, amplified, and monitored with an oscilloscope and a loudspeaker. Discharge patterns were recorded on a storage oscilloscope (Tektronix 5103N) with the amplified signal on the z-axis and time on the x-axis. A sweep was triggered by the onset of a stimulus, so that one response appeared as one row of bright spots on the screen. The screen was photographed with a Polaroid camera; from these photographs the Figures were re-drawn.

The optical system had two channels where interference filters (Schott DIL), neutral density filters and wedges could be inserted independently. One channel was used for full-field bleaches and backgrounds (diam. 4·8 mm on the retina), the other for stimulation. The optical system and the recording technique were basically as described by Donner & Reuter (1968) and Bäckström, Hemilä & Reuter (1978).

Receptive fields were localized with various stimuli against a dim red background and cells were classified with adequate stimuli according to Maturana, Lettvin, McCulloch & Pitts (1960). For this paper only on-responses were used, and the cell classes studied were class 3 and classes 1 and 2, which, in the present experiments, did not behave differently and are therefore considered together (sustained cells). For the actual recordings the cells were stimulated with circular 513 nm step stimuli given once every 30 sec or 1 min. The usual duration was 5 sec, but at high intensities it was shortened to even 0·5 sec (where this did not affect the on-response) in order to minimize the adapting effect. The log intensity scale in the Figures directly gives log (number of quanta)/(sec . mm^2) incident on the retina.

RESULTS

The spatial arrangement of the receptive field: area-threshold measurements

One way commonly used for characterizing the spatial extents and relative sensitivities of the excitatory and inhibitory mechanisms is to measure the ganglion cell threshold as a function of the area of the stimulating spot (Barlow, 1953). As frog ganglion cells are usually completely silent when not stimulated, the on-threshold was here taken as the lowest stimulus intensity regularly evoking at least one spike within the 5 sec the light was kept on. With small central spots it is a good measure of excitatory sensitivity. With large spots extending into the inhibitory surround such a threshold has generally been considered to reveal the excitation/inhibition balance. Accepting this assumption for the moment, disregarding questions of the possible meanings of a threshold determined by antagonistic signals with different temporal properties (cf. Donner, 1981), the area-threshold curves in Fig. 1 may characterize the functional arrangement of the receptive field in dark- and light-adapted states. Thresholds always get lower in roughly inverse proportion to area up to a certain

point. A further increase in area usually has little effect in the *dark-adapted* receptive field (Fig. 1*A* and upper curve in Fig. 1*B*). Thus the spatial arrangement of the excitatory mechanism may be crudely described as an equisensitive, approximately circular plateau with sharp borders. In the Figure, this amounts to fitting a 45° line to the points for small spots and a horizontal line to the points for larger spots

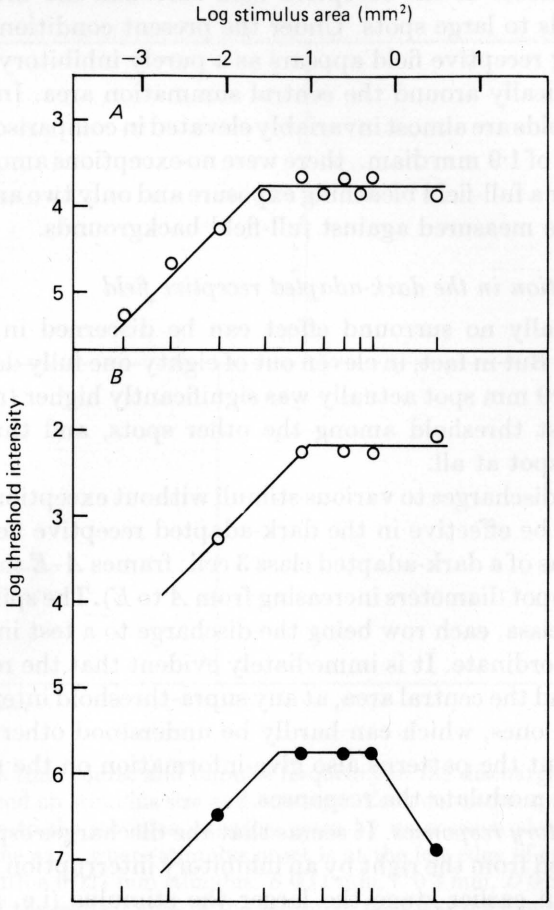

Fig. 1. Area-threshold relation of (*A*) a dark-adapted cell (sustained); (*B*) another cell (class 3), open symbols, dark-adapted; filled symbols, 25 min after a 3% rhodopsin bleach. Ordinate, log threshold intensity; upper abscissa, log stimulus area (mm²). The unevenly spaced marks on the lower abscissa refer to each of the stimulus sizes used: their diameters were 0·027, 0·051, 0·11, 0·18, 0·3, 0·41, 0·53, 0·67, 0·80 and 1·9 mm. In these experiments, stimuli were presented at 0·2 log unit intensity intervals and the lowest intensity evoking at least one spike on at least half of the trials (both when approached from higher and from lower intensities) was regarded as threshold.

(indicating complete summation and no summation respectively). The point of intersection may be taken as an estimate of the border of the central area (cf. Cleland & Enroth-Cugell, 1968), the excitatory receptive field. Mean diameters thus obtained were 0·26 mm for the (ten) class 3 cells and 0·22 mm for the (fifteen) sustained cells reliably classified from which complete area–threshold curves were measured.

Light-adaptation, whether with a background or as in Fig. 1*B* by bleaching pigment, has two effects: (1) the central summation area of the receptive field shrinks somewhat even in the rod range, finally reaching its cone-determined size (mean diameters 0·21 mm for class 3 and 0·15 mm for sustained cells as reported by Bäckström & Reuter (1975), whose frogs represented the same population as those used here); (2) the effects of the receptive field surround are brought out as an elevation of thresholds to large spots. Under the present conditions of stimulation, the surround of a frog receptive field appears as a purely inhibitory region arranged more or less concentrically around the central summation area. In a light-adapted eye, large-spot thresholds are almost invariably elevated in comparison with 'optimal' spots: with a stimulus of 1·9 mm diam., there were no exceptions among twenty-seven cells investigated after a full-field bleaching exposure and only two among twelve cells whose thresholds were measured against full-field backgrounds.

The presence of inhibition in the dark-adapted receptive field

As mentioned, usually no surround effect can be discerned in a dark-adapted area–threshold curve. But in fact, in eleven out of eighty-one fully dark-adapted cells the threshold to the 1·9 mm spot actually was significantly higher (more than 0·5 log units) than the lowest threshold among the other spots, and three cells did not respond to the large spot at all.

The actual impulse discharges to various stimuli without exception show inhibition from the surround to be effective in the dark-adapted receptive field. In Fig. 2 are seen discharge patterns of a dark-adapted class 3 cell; frames *A*–*E* show the responses to one test spot each (spot diameters increasing from *A* to *E*). The spikes are displayed as dots on a time abscissa, each row being the discharge to a test intensity given by its position along the ordinate. It is immediately evident that the responses to large spots extending beyond the central area, at any supra-threshold intensity, are weaker than those to smaller ones, which can hardly be understood otherwise than as the effect of inhibition. But the patterns also give information on the manner in which inhibition intrudes to modulate the responses.

Pre- and post-inhibitory responses. It seems that the discharges especially at higher intensities are devoured from the right by an inhibitory interruption, which at a given intensity sets in at an earlier stage the larger the stimulus (i.e. the stronger the stimulation of the inhibitory mechanism). The discharges seem to consist of an initial 'undisturbed' burst possibly followed by a few stray spikes. The burst may be regarded as 'undisturbed', or *pre-inhibitory*, because its spike frequency is not affected by the degree of stimulation in the inhibitory region of the receptive field (see Fig. 3). But the *length* of the burst not only generally depends on the strength of inhibition, it also varies with stimulus intensity in different ways depending on how strongly inhibition is activated. In the responses to small spots (Fig. 2*A*, *B*) the burst gets longer towards lower intensities, in those to an intermediate spot (Fig. 2*C*) it remains more constant, while in large-spot responses it gets shorter (Fig. 2*D*). That is, the time of the apparent onset of inhibition depends on stimulus intensity and area covering the inhibitory mechanism, just as is the case for excitation.

In the responses to large spots there is in fact an intensity below which the cell ceases to give any responses of an impulse frequency and latency comparable to those

elicited with smaller spots (in Fig. 2*D* log intensity 6). Whereas the spot in Fig. 2*D* still evoked responses consisting of a few stray spikes below that intensity, the largest spot most efficiently stimulating the inhibitory surround (Fig. 2*E*) elicited a couple of fast spikes only at the very highest intensities and no responses at all below log intensity 7·5, except just at the absolute threshold (in this cell log intensity 3,

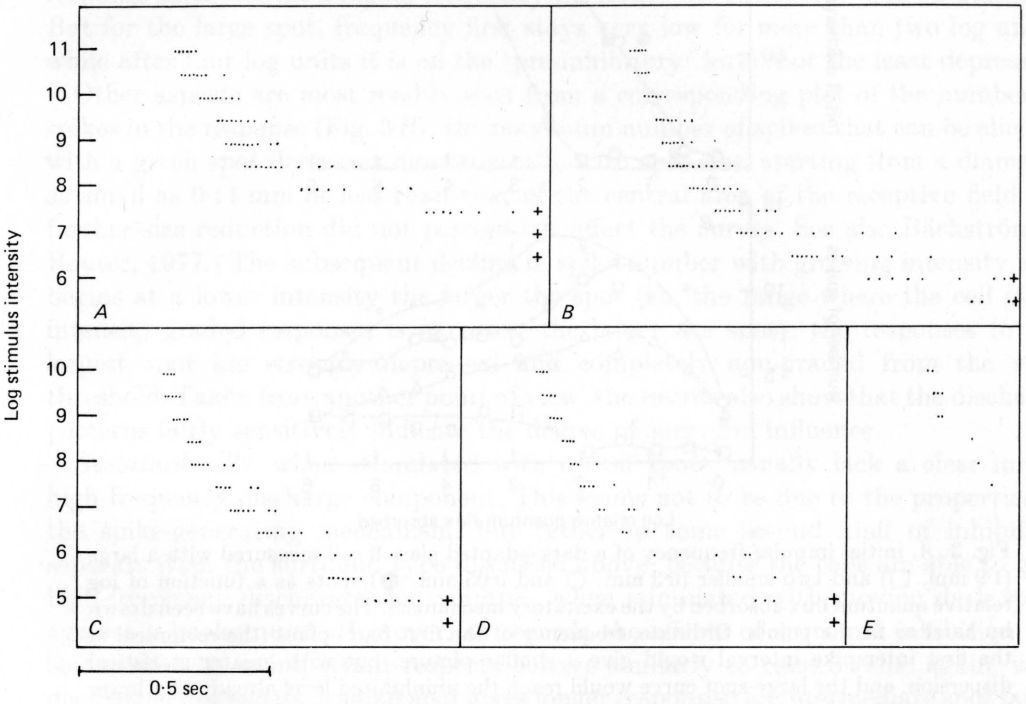

Fig. 2. How the time course and impulse frequency of the discharges of a dark-adapted class 3 cell depend on stimulus size and intensity. Each dot is one spike, each row of dots is one discharge to the stimulus intensity given by its position along the ordinate. The abscissa is a time axis, where stimulus onset is at the left edge of each frame. Frame *A* was recorded with a 0·027 mm stimulus, *B* 0·11 mm, *C* 0·3 mm, *D* 0·8 mm and *E* 1·9 mm; the diameter of the central area of the receptive field was 0·3 mm. The + signs signify that the discharge continued with spikes not included in the Figure. Responses were recorded with 0·5 log unit intensity intervals from threshold up to an intensity arbitrarily chosen. Threshold was log intensity 3 in *C*–*E*; responses having too long latency have not been included.

not shown in the Figure). The exact spot size required for a certain inhibitory effect varied from cell to cell, but the general picture was always the same: for all spots sufficiently stimulating the surround there was an intensity below which the responses either changed their character as in Fig. 2*D*, or disappeared altogether, or, the intermediate case, there was a broader or narrower silent range of intensities where no responses could be obtained, while at the very lowest intensities it was again possible to evoke some spikes. All this seems to imply two things. First, that whether thresholds are actually raised or not, the inhibitory surround is active even at the

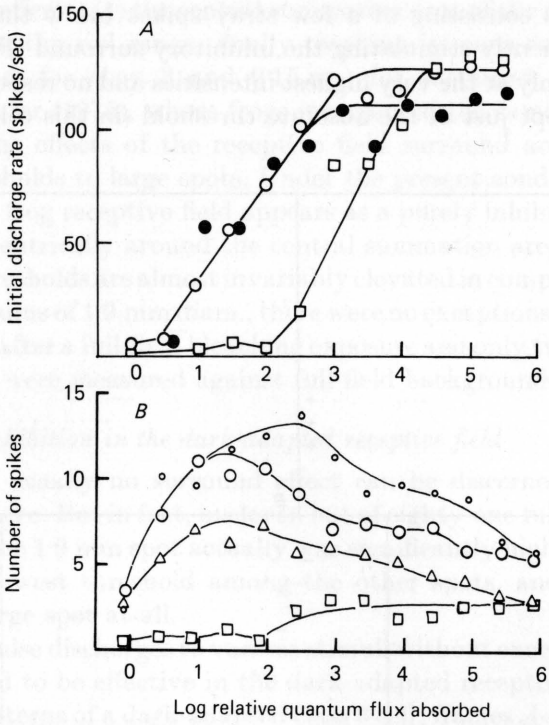

Fig. 3. *A*, initial impulse frequency of a dark-adapted class 3 cell measured with a large (1·9 mm, □) and two smaller (0·3 mm, ○ and 0·05 mm, ●) spots as a function of log relative quantum flux absorbed by the excitatory mechanism. The curves have been drawn by hand to fit the points. Ordinate, frequency of the first four spikes (the reciprocal of the first interspike interval would give a similar picture, but with greater statistical dispersion, and the large-spot curve would reach the uninhibited level already at a lower intensity). The abscissa has been calculated on the assumption that the ganglion cell *threshold* always corresponds to equal flux absorbed by the excitatory mechanism, regardless of spot size (as long as there is no inhibitory threshold elevation; the threshold to the large spot in the Figure was not elevated). This is justified by the summation properties shown by area–threshold curves (see section 1 of this paper) and also by the agreement between these and the summation properties shown by supra-threshold response latencies (Donner, 1981). Then log relative flux absorbed can be calculated as log (stimulus intensity)/(threshold intensity). The size of the central area of the receptive field was 0·24 mm. *B*, the total number of spikes in the response of class 3 cells (averaged) as a function of log relative quantum flux absorbed by the excitatory mechanism. Each curve is based on measurements with one stimulus size, diameters 0·11 (○), 0·3 (○), 0·8 (△) and 1·9 (□) mm. Every point is the mean of measurements from 5–7 cells, each first plotted on an abscissa as in Fig. 3*A*. The averaging was done because of the comparatively great variation in the number of spikes between individual responses.

very lowest stimulus intensities (threshold was often less than 3 quanta/sec absorbed by the excitatory mechanism). Secondly, that the large-spot responses obtained at low intensities are quite distinct from the high-intensity responses. They obviously do not precede, but rather break through inhibition, and will therefore be termed *post-inhibitory* responses.

The fact that it is possible to distinguish between two response types will prove

important for understanding threshold changes during bleaching adaptation. Therefore, to support this conclusion, the initial discharge rate of a class 3 cell has been plotted in Fig. 3*A* as a function of the relative log quantum flux absorbed by the excitatory mechanism, for three different test spot sizes (for the determination of flux, see Figure legend). The impulse frequency of a pure excitatory, pre-inhibitory burst is seen to be almost proportional to the log flux absorbed up to the point where the response saturates (at a higher frequency the larger the excitatory area stimulated). But for the large spot, frequency first stays very low for more than two log units, while after four log units it is on the 'pre-inhibitory' level, not the least depressed.

Other aspects are most readily seen from a corresponding plot of the number of spikes in the response (Fig. 3*B*): the maximum number of spikes that can be elicited with a given spot decreases monotonically with spot size, starting from a diameter as small as 0·11 mm or less than that of the central area of the receptive field. (A further size reduction did not perceptibly affect the curves. See also Bäckström & Reuter, 1977.) The subsequent decline in spike number with growing intensity also begins at a lower intensity the larger the spot (i.e. the range where the cell gives intensity-graded responses is narrower the larger the spot); the responses to the largest spot are strongly depressed and completely non-graded from the very threshold. Taken from another point of view, the results also show that the discharge patterns fairly sensitively indicate the degree of surround influence.

Sustained cells, when stimulated with on–off spots, usually lack a clear initial high-frequency discharge component. This seems not to be due to the properties of the spike-generating mechanism, but rather to some second kind of inhibition separate from the surround type discussed above, because the cells are able to give high-frequency discharges, for example, when stimulated with moving dark spots against a background. However, as regards the effects of surround inhibition the sustained cells in important respects behave similarly to class 3 cells: again, with decreasing intensities, a small spot gives longer responses, an intermediate spot fairly constant responses, while the responses to a large spot get shorter, then disappear or are converted into long-latency 'post-inhibitory' responses.

Bleaching adaptation: thresholds and discharge patterns

In the first section, following Barlow *et al.* (1957), the effects of a bleach and those of a steady background on the potency of the surround have not been distinguished. As they are in fact rather different, they will be treated in separate sections.

In the cat, a bleach causes thresholds to large spots to be strongly elevated during the initial phase of dark-adaptation, thus revealing the surround. At some stage not related to the cone-rod shift there is a sudden transition to the dark-adapted situation, i.e. large-spot thresholds drop rather abruptly. These observations were seen to hold for the frog as well. Then, in order to see in more detail how the functioning of the receptive field is modified, whole series of responses (as functions of stimulus intensity) were registered at different times during the course of dark-adaptation. The results of one such experiment are shown in Fig. 4. To the right are shown the threshold adaptation curves, as measured with a 1·9 and a 0·11 mm spot, and to the left the actual discharge patterns to a series of supra-threshold stimuli. If the large-spot threshold drop actually reflected a correspondingly dramatic

desensitization of the inhibitory mechanism, one would expect this to show up in the discharge patterns. However, there is no obvious change in the responses to higher intensities in connection with the apparent release from inhibition. Rather, there appears a new distinct low-intensity range giving long, irregular responses, which in this case remain separated from the high-intensity ones by a silent range (in the way mentioned earlier).

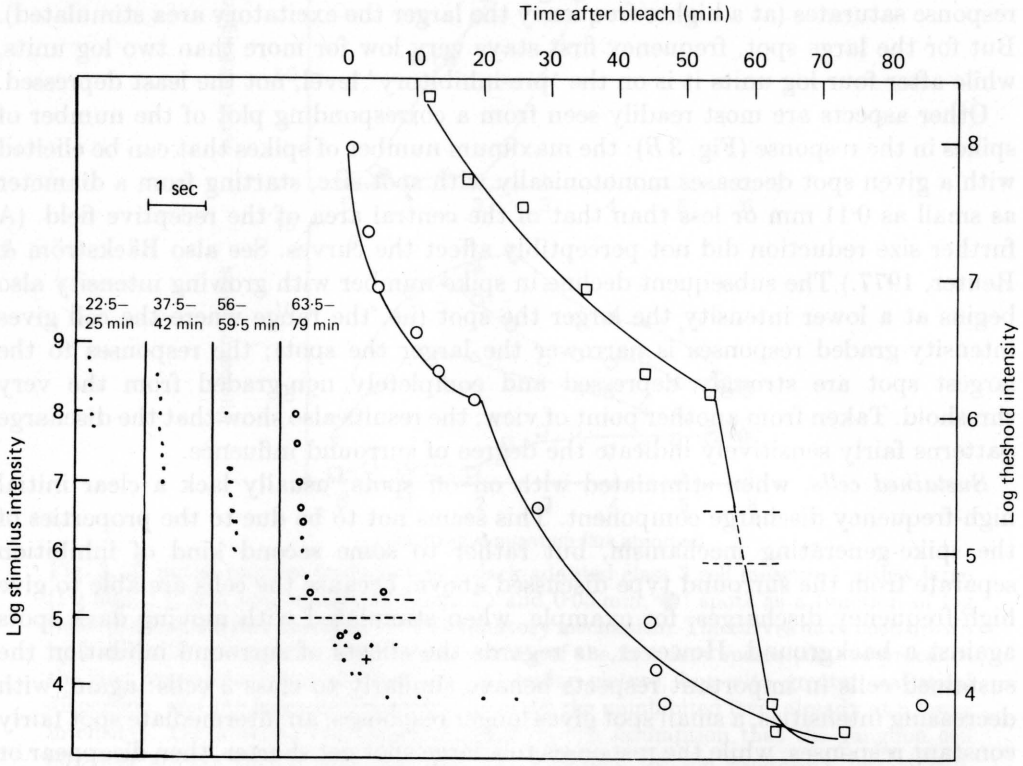

Fig. 4. Threshold adaptation curves measured with a 0·11 mm (○) and a 1·9 mm (□) test spot after a 3 % bleach, and response patterns for the latter spot recorded at different times during the course of adaptation. The response patterns are displayed as in Fig. 2; above each series of patterns is given the time interval during which it was recorded. The dashed lines mark the range where no responses could be obtained with the large spot. In the patterns of 63·5–79 min, spikes recorded during the last 10 min are represented by small circles. Temperature was kept as low as 7·5–8·8 °C to minimize adaptation during pattern recording. Sustained cell.

The threshold drop was often as abrupt as in Fig. 4, especially in sustained cells, spanning even 3 log units within 5 min. It is difficult to get a more precise idea of its rapidity, because it usually takes a few minutes to get a reliable threshold determination (and, in the case of such great drops, to find the right range of stimulus intensities). But in other cells the transition was more protracted (up to some 10–15 min), in the start not accompanied by the appearance of a long-latency response type. And finally, in cells with strong inhibition, giving no responses to low intensities even in the dark-adapted state, there was of course never any threshold drop. In such cells the large-spot thresholds turned out to be elevated relatively most in the dark-adapted state.

Adaptation by steady backgrounds

Although light-adaptation with steady backgrounds does also cause a relative elevation of thresholds to large spots, the effects are generally weaker and, above all, more gradual than those produced by a bleach. Partly different mechanisms must be involved: while the average elevation after a full-field bleach was 1·5–2 log units, it was only 0·5–1 log unit against full-field backgrounds. Fig. 5 shows results from

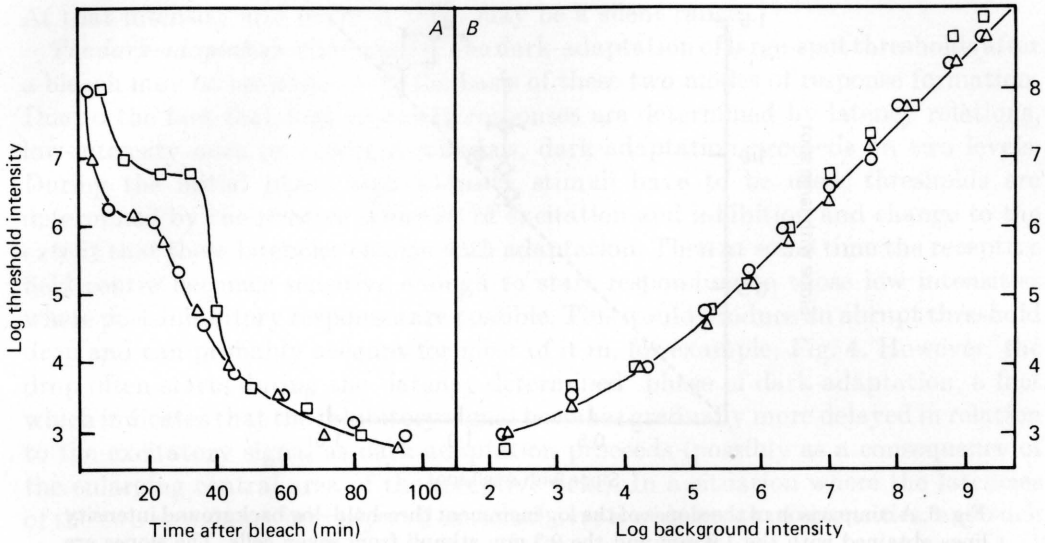

Fig. 5. The different effects of bleaching adaptation and background adaptation on threshold. The threshold of a class 3 cell was first followed after a full-field 3 % bleach (*A*), then against successively increased 558 nm full-field backgrounds (*B*). Stimuli were 513 nm spots with diameters 0·3 mm (○), 0·8 mm (△) and 1·9 mm (□). When the increment thresholds against backgrounds had been measured, the retina was bleached anew and it was ascertained that the differences did not depend on some general deterioration of the inhibitory mechanism. The central summation area of the receptive field had a diameter of 0·3 mm in the dark-adapted state.

a cell, where successively increasing backgrounds little affected large-spot thresholds, while after a 3 % bleach these were initially raised by as much as 2 log units.

Part of the relative elevation may be produced by rather weak backgrounds, already before the Weber range. However, without doubt there still is an increasing tendency towards further elevation as background intensity is raised. This is seen by comparing the slopes of the straight lines of increment threshold plots. Fig. 6 shows the relation between the small-spot and the large-spot slopes for the seven cells on which adequate measurements were made with both. In all cases the large-spot slopes were greater, but in only three were they significantly so. The material is insufficient to establish a clear correlation between cell classes and the adaptational behaviour of large-spot thresholds, but sustained cells did seem to be more susceptible to light-adaptation. The mean small-spot slope (twelve cells) was 0·9 in agreement with the value obtained by Hemilä (1977) for the rod receptor potential.

DISCUSSION

The purpose of this work was to study what kinds of changes in organization in the receptive field must be postulated to explain the light-dark-adaptation of thresholds and how far it can be accounted for in terms of receptor adaptation, with invariant receptive field properties. As it turned out, the actual discharge patterns gave no indications of the fundamental change in receptive field functioning that one

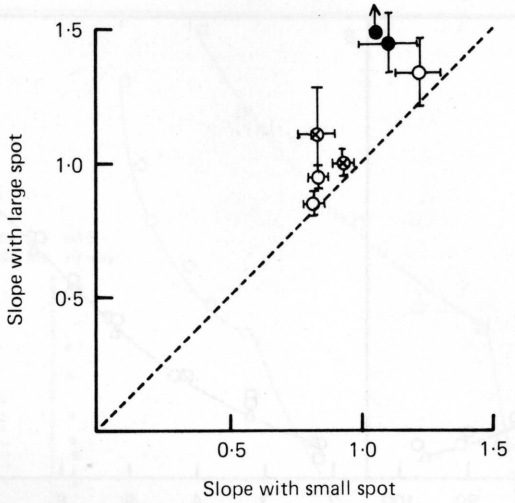

Fig. 6. A comparison of the slopes of the log increment threshold–log background intensity lines obtained with the 1·9 mm and the 0·3 mm stimuli from seven cells. The slopes are regression coefficients calculated on the basis of the data points lying between 5 and 9 log units background intensity. The bars give the standard deviations of the coefficients. ●, refer to sustained cells; ○, to class 3 cells and ⊕, to cells not classified.

would expect from threshold measurements. Two effects have generally been taken as indications of the weakening of the surround with dark-adaptation. One is the peculiar behaviour of large-spot thresholds after a bleach, not actually reinvestigated after the original report by Barlow *et al.* (1957). The other is the steeper rise of increment threshold lines when measured with large spots confirmed by Barlow & Levick (1976). The two phenomena, not simply linked (Fig. 5), will be discussed separately.

Bleaching adaptation

Latency and strength of inhibition. If the inhibitory signal is to systematically extinguish a response, e.g. elevate a threshold, it must be at least as strong as the excitatory signal *and* it must arrive at the ganglion cell at least simultaneously. The occurrence of a response means that inhibition has failed in either (or both) of these respects. From the discharge patterns of class 3 cells it appeared that the responses to large spots can be divided on this basis into two separate intensity ranges. At high test intensities the main response component is pre-inhibitory and the *timing* of the inhibitory signal is all-important. The initial discharges then have latencies and spike frequencies similar to those obtained with smaller spots, but are sharply interrupted

by the onset of inhibition. Elsewhere (Donner, 1981) I have suggested a hypothesis to describe how the relative timing of excitation and inhibition depend on the quantum flux absorbed by the respective mechanisms, as well as on the state of adaptation (the latter inducing a general latency change common to the two mechanisms). On the other hand, the strongly depressed low-intensity responses to large spots are clearly post-inhibitory (further discussed below); for these mainly the strength relations of excitation and inhibition are important. The border between the two ranges is a test intensity where excitation and inhibition arrive simultaneously. At that intensity and below it there may be a silent range.

The dark-adaptation of thresholds. The dark-adaptation of large-spot thresholds after a bleach may be understood on the basis of these two modes of response formation. Due to the fact that high-intensity-responses are determined by latency relations, low-intensity ones by strength-relations, dark-adaptation proceeds on two levels. During the initial phase high-intensity stimuli have to be used, thresholds are determined by the relative latencies of excitation and inhibition and change to the extent that these latencies change with adaptation. Then at some time the receptive field centre becomes sensitive enough to start responding to those low intensities where post-inhibitory responses are possible. This would produce an abrupt threshold drop and can probably account for most of it in, for example, Fig. 4. However, the drop often starts during the 'latency-determined' phase of dark-adaptation, a fact which indicates that the inhibitory signal becomes gradually more delayed in relation to the excitatory signal as dark-adaptation proceeds (possibly as a consequence of the enlarging central area of the receptive field). In a situation where the latencies of the two signals are initially well matched over a wide range of intensities, any such change in relative latencies would be greatly amplified with regard to threshold.

The origin of post-inhibitory spikes

The absence of post-inhibitory firing at higher intensities suggests that the excitation/inhibition balance is dependent on stimulus intensity. However, the difference may be given a purely statistical explanation:

If n is the mean number of photons absorbed by the central area of the receptive field (or the inhibitory region) within a certain time, then (due to quantal fluctuation) the amount of excitation (or inhibition) reaching the ganglion cell will show a relative fluctuation proportional to $n^{-\frac{1}{2}}$. Because of this there is a certain probability that, at some moment, the net signal will be excitatory even when inhibition is stronger on an average. This is important at *low* intensities for two reasons: (1) the relative fluctuation grows with decreasing n. Near the absolute threshold, with a *total* of some 10–20 quanta absorbed within the integrating time (about 5 sec), it may be considerable; (2) at the lowest intensities in the dark-adapted eye the receptor signals are slowly rising and sustained (cf. Hemilä, 1977); excitation itself is more sustained and the extended time scale gives a higher probability of spikes getting through. And finally, the inhibitory signal is obviously most effective when appropriately timed; it certainly does occur that spikes break through if inhibition precedes excitation too much (Nye & Naka, 1971), as may be the case at the lowest intensities (Donner, 1981).

Background adaptation

The results shown in Fig. 6 essentially agree with those of Barlow & Levick (1976), even to the extent that the transient (class 3, 'Y') cells seem to show less large-spot elevation than the sustained (class 1–2, 'X') cells. It is obvious that the tendency of backgrounds gradually to raise large-spot thresholds more than small-spot ones is an effect quite different from the threshold jumps induced by a bleach (although these may of course conceal smaller, more gradual changes). Whether the difference lies in the receptors or in the network cannot be decided from the present results. It is even possible that the effects of backgrounds depend simply on the shrinking of the central receptive field area with light adaptation, relatively enfeebling the excitatory mechanism.

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