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CENTER AND SURROUND EXCITATION IN THE RECEPTIVE FIELDS OF FROG RETINAL GANGLION CELLS

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Abstract—We have reexamined the receptive fields of frog retinal ganglion cells focussing on their surround properties. Carefully excluding artifacts due to stimulation of the (Gaussian) RF center, we found that spiking responses can be elicited by step stimulation of any receptor type in the surrounds of all the classes 1–4 Maturana *et al.* (1960) (*J. gen. Physiol.* **43**, 129–175). The surround responses are antagonized by the responsive center and suppressed by the inhibitory surround, but are seen because of their slower dynamics. The responsive surround differs spectrally from the center: in the latter, cones and green rods compete, in the former, their signals sum.

Retina Ganglion cell Receptive Field Surround antagonism Frog

INTRODUCTION

The prevalent notion of the receptive field (RF) of a frog retinal ganglion cell is still that formulated by Barlow (1953): a well-defined excitatory center responding either to the onset or the offset of illumination, or to both, concentrically surrounded by a silent zone of inhibitory net effect counteracting all ganglion cell discharges. Correspondingly, the Grüsser and Grüsser-Cornehls (1973) model involves two mechanisms: (1) an excitatory (center) mechanism (on, off or on-off) and (2) a purely inhibitory one always acting to suppress impulse discharges, never producing any. Both mechanisms are described as spatially Gaussian-distributed around a common midpoint, but given the lower peak and wider spread of the inhibitory mechanism, they add up to an excitatory center (ERF) plus inhibitory surround (IRF). This is in sharp contrast to the RF arrangement in the retina of e.g. the cat (Kuffler, 1953) and of many other vertebrates, where stimulation of the RF periphery not only antagonizes center responses, but also evokes complementary (surround) responses. We shall here use the terms *inhibitory* and *lateral inhibition* for a surround mechanism which exclusively acts to suppress any impulse discharges from the ganglion cell, and the term *responsive* for a surround mechanism which may in itself cause the ganglion cell to fire (the responsive surround may of course in addition be *antagonistic* to the center).

The Barlow RF model has been questioned earlier, notably by Keating and Gaze (1970) and Morrison (1975a, b) who were able to elicit spikes by stimulation outside the apparent RF center in off-center and on-off-center cells respectively. Zhukov (1980) found alternating inhibitory and facilitatory zones in the surround, using moving stimuli. However, the question of a responsive surround has remained controversial. First, when the periphery of the RF is stimulated, it is unavoidable that the center is simultaneously stimulated to a degree difficult to assess (by stray light and, possibly, by direct illumination of the tails of the center sensitivity distribution). Secondly, apparent surround responses may in fact originate in the green rods, known to form excitatory receptive fields much larger than the center proper mediated by cones or red rods (Bäckström and Reuter, 1975). Thirdly, the occurrence of surround responses in the different classes of the Maturana, Lettvin *et al.* (1960) classification has not been systematically explored.

In the present work we show that a responsive surround, antagonistic to the center, but distinct from the inhibitory surround, is indeed a normal feature of the RFs of all the ganglion cell classes 1–4. In some class 1, 2 and 3 cells this creates an on-off-center, off-on-surround organization with superposed inhibitory on and off mechanisms.

METHODS

Recording and stimulation

Spike thresholds and response patterns were recorded extracellularly from the eyecup of *Rana temporaria*. Through a two-channel optical system, where filters could be independently inserted, different stimuli were presented against different backgrounds. For a fuller account of recording and stimulation techniques, see Donner and Reuter (1968) and Bäckström *et al.* (1978).

In this work it was particularly important to be sure that responses evoked by stimulation of different, more or less distant points on the retina actually originated in the same cell. As the ratio spike

amplitude/noise amplitude usually exceeded 10 in our recordings, cells were easy to recognize from the features of their spikes—it is most unlikely that two cells go on for a long time giving spikes indistinguishable in amplitude and shape. The good isolation of spikes in our recording system in fact meant that in some 80% of all cases only one cell at a time rose above noise level. The few experiments where we could not be absolutely sure were discarded.

Receptive fields were localized and cells classified with adequate stimuli (cf. Maturana *et al.*, 1960) against a dim 615 nm background. In the actual recordings, the stimuli used were either circular spots centered on the receptive field (diameters on the retina: 0.027, 0.051, 0.11, 0.18, 0.3, 0.53, 0.67, 0.8, 1.9 and 4.6 mm) or, for selective stimulation of the surround, annuli of various inner and outer diameters concentric with the receptive field. Unless otherwise stated, both the inner and outer diameter were always equal to one of the spot diameters enumerated above. All stimuli were given as on-off steps (usually 5 sec duration at 30 sec intervals).

The contributions from the main receptors (red rods, peak absorption at 502 nm, single cones, 580 nm, and green rods, 433 nm) were separated by using different backgrounds and stimulus wavelengths (Schott and Gen, DIL filters): (1) the red rods were studied in fully dark-adapted eyes without the use of backgrounds. By their absolute sensitivity it was possible to exclude other receptors; (2) cones and green rods were both studied under a 558 nm background just saturating the red rods [$3 \cdot 10^{10}$ quanta·(sec·mm^2) incident on the retina, see Donner and Reuter (1968)], using 615 nm stimuli for the cones and 435 nm stimuli for the green rods. Against the background used, the former wavelength virtually fails to stimulate the green rods, while the green-rod-mediated responses are some 2.5 log units more sensitive to the latter wavelength than are the cone-mediated ones (Bäckström and Reuter, 1975). In some experiments, where full spectral sensitivity curves were measured (wavelengths used: 396, 416, 435, 454, 476, 495, 513, 533, 553, 577, 596, 615, 639, 661 nm), the intensity of the background was raised tenfold in order to suppress the red rods more firmly still.

The intensity scales of the Figures express absolute stimulus intensities directly in photons incident on the retina/(sec·mm^2).

Classification of cells

Of the 82 light-adapted cells studied, 76 were readily accommodated in one of the classes of Maturana *et al.* (1960) (c.f. also Bäckström and Reuter, 1975); the 6 aberrant cells are treated separately in the Results section. Here we shall only briefly describe the response properties used for classifying the cells (referring to conditions where the green rods are not stimulated).

Class 1–2 (sustained) cells. For our purposes, the two first classes of Maturana *et al.* (1960) behaved very simularly, and following Keating and Gaze (1970) we treated them as one group. They are on-off-center cells, responding particularly well to small moving dark or light spots. The distinctive features on which our classification was based were: (1) the maintained discharge lasting several seconds after a small moving dark spot was stopped in the RF center; (2) the virtual absence of responses to full-field changes in illumination, showing the strong inhibitory surround of these cells. Usually they are easily distinguished from class 3 cells also by their typical long low-frequency discharges in responses to small-spot step stimuli.

Class 3 cells are also on-off-center cells, but are distinguished from class 1–2 cells by their brisk responses to long straight moving edges and full-field steps of light or darkness, indicating i.a. a weaker lateral inhibition. They do respond to most of the stimuli effective on class 1–2 cells, but instead of sustained discharges give high-frequency transient bursts.

Class 4 cells are off-center cells responding with long and strong discharges to any decrease in the illumination of the RF center. Unless the green rods are stimulated, they never give on-responses to center stimulation. Their inhibitory surround is so weak that the threshold of the off-responses is typically equally low to a full-field stimulus as to a spot optimally matching the RF center.

In the course of this study we encountered no pure on-center cells, but we did find a few cells resembling Maturana *et al.*'s *class 5* (dark detectors) characterized by a maintained discharge decreasing with illumination of the RF center. These were not studied systematically; only one seemed to possess a clear surround (enhancement of ongoing discharge at center off or surround on, suppression at center on or surround off).

Evaluation of light scatter

The level of accidental light scatter on to the receptive field center when peripheral stimuli are used is of crucial importance in these experiments. To get as accurate an estimate as possible we employed two methods: (1) direct measurement of the light intensity in the center of annuli (with no eyecup in place) with an Airam UVM-8 calibrated light meter. Unfortunately the aperture of the detector allowed reliable measurements only of annuli with inner diameter no less than 1.9 mm. Keeping this constant, we varied annulus area by varying the outer diameter. Scatter turned out to depend fairly strongly on area, being 4% of the direct light intensity for an outer diameter of 3 mm and 10% for full-field illumination with only the 1.9 mm circle eclipsed. (2) To get an independent estimate (and one corresponding to the real experimental situation, including i.a. intraocular scatter), we used the response latency method (see

Donner 1981a and the Results section below). We recorded complete stimulus intensity—response latency functions from the same ganglion cell first for a stimulus spot fully covering the excitatory receptive field center, then for an annulus of outer diameter 1.9 mm and inner diameter just above that of the center. At *high* stimulus intensities the annulus elicited short-latency responses of obvious center origin due to stray light. The latencies of high-intensity responses are practically unaffected by inhibition and are unique functions of the photon flux absorbed by the receptive field center (Donner, 1981a). By comparing response latencies to the spot and the annulus, one can express the flux on the whole receptive field center produced by the annulus as a fraction of the flux produced by the spot. We did this on nine ganglion cells and found a mean scatter of $5.9\% \pm 0.5\%$ (SEM). In the range of annulus inner diameters from 0.3 to 0.8 mm we found no correlation between inner diameter and light scatter. It should be added that these measurements were done in a situation where the image on visual inspection looked sharply focussed. Before and after each experiment focussing was checked through a microscope and optically unsatisfactory experiments were discarded.

To avoid all uncertainty about light scatter we adopted the following restrictions on the annuli used for *identifying* surround responses: we never used outer diameters above 1.9 mm and never inner diameters below 0.53 mm. And to avoid as far as possible direct stimulation of the center mechanism we always used an inner diameter at least one number bigger (in the set enumerated above) than that for which the area-threshold curve of the cell under study reached its horizontal plateau (see the first section of the Results). We made exceptions from these rules only where annulus dimensions were not crucial.

The application of drugs

In some experiments we applied picrotoxin or/and strychnine to suppress inhibitory connections based on GABA or glycine as transmitters. The concentrations and procedure used were such as have previously been shown to suppress efficiently different types of inhibition in the same preparation (Bäckström, 1981; Grönholm and Reuter, 1981), and the reader is referred to these papers for details. The drug was applied as a 1 μl drop into the layer of vitreous remaining in the eyecup, the solutions used being picrotoxin: 0.5 mg/ml Ringer, strychnine: 1 mg/ml Ringer, Ringer: 95 mM NaCl, 3 mM KCl, 0.9 mM $CaCl_2$, 0.5 mM $MgCl_2$, 12 mM Na-phosphate buffer, pH 7.5.

RESULTS

Delimiting the center mechanism

In the frog, in contrast to mammals, the receptive field (RF) center of most ganglion cells can respond to both the onset and the offset of a light, and so the demonstration of separate surround responses is not simple. Without knowledge of cellular pathways there are two conceivable ways: either it can be shown that peripheral stimuli elicit discharges even when the photon flux absorbed by the center is subthreshold, or it can be shown that the responses elicited by peripheral stimuli have some special properties, e.g. different spectral sensitivity. We shall use the straightforward first way as criterion (and then proceed to show that the surround responses also do have special properties). This requires a meticulous mapping of the central sensitivity distribution, for which there are several traditional methods (Hartline, 1938; Barlow, 1953; Bäckström and Reuter, 1982): (1) measuring thresholds to a small spot at different positions in the RF; (2) moving a spot or a contour in different directions against a background and recording its positions when the cell starts or stops firing; (3) area-thresholds curves, i.e. recording threshold intensity as a function of the area of a stimulating spot centered on the RF. At the outer margin of the sensitivity distribution, the region most important in the present context, all these methods suffer from an uncontrollable lateral inhibitory influence apparently producing a misleadingly steep fall-off at the edges (Stell *et al.*, 1974; Bäckström and Reuter, 1982). The area-threshold measurements should be least affected, as they always include stimulation of the region of maximum sensitivity, so we chose them for our point of departure. The circles in Fig. 1 show exemplary results from a dark-adapted (A) and a light-adapted (B) cell. The area-threshold functions consist of an initial slope with approximate trade-off between stimulus area and threshold intensity levelling off to a horizontal portion where threshold intensity remains more or less constant, independent of area. Particularly in the light-adapted state this is—with still larger stimuli—followed by a section where threshold intensities may *rise* with growing area because of inhibition.

The obvious interpretation of the horizontal part is that here the stimuli already extend beyond the borders of the RF center, so that a further extension no longer affects the degree of center stimulation. The zone of transition from a sloping to a horizontal line would then mark the border of the center. However, it might be argued that even the entire horizontal part is suppressed by inhibition concealing the real extent of the center.

To come to grips with such an argument we used another method of obtaining an area-sensitivity function: response latency. The basis for this is the fact that response latency shortens in a predictable way as a function of the *quantal flux absorbed* by the center mechanism (Donner, 1981a). This implies that the same effect on latencies can be achieved either by, say, doubling stimulus intensity or by doubling the effective stimulus area [i.e. the integral of (area

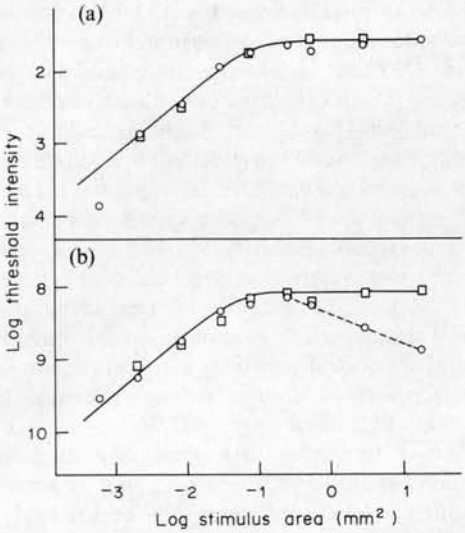

Fig. 1. Area-sensitivity functions of the center mechanism of two cells, one dark-adapted (a), the other light-adapted by the usual 558 nm background (b). The abscissa gives log area (mm^2) of the stimulating spot, the ordinate gives log threshold intensity (quanta·sec^{-1}·mm^{-2} incident on the retina). Circles give response thresholds; the intensity scale refers to these. Squares give relative sensitivities measured with the latency method (see the text); the family of squares is arbitrarily placed on the intensity scale for best coincidence with the circles in the small-spot region. Stimuli were 513 nm in (a) and 615 nm in (b); only on-responses were used. The curves, vertically placed to fit the points, are cumulative Gaussians with $\sigma = 0.085$ mm.

covered)·(relative sensitivity)] keeping intensity constant. If the *spatial* expansion of the stimulus necessary for a latency-match with a certain *intensity* increase is measured, the underlying spatial sensitivity distribution can be inferred. The advantage of this procedure is that response latencies to high stimulus intensities are little, if at all, affected by inhibition (Donner, 1981b). So, first the whole stimulus intensity—response latency function is determined for each spot, then the *shifts* required (rightwards on a log intensity scale) to make all the curves for bigger spots coincide with that obtained for the smallest one. That shift is a measure of the sensitivity increment due to the expansion of the stimulus spot, and if it is plotted against log area, a (relative) area–sensitivity function arises. In Fig. 1 the results have been plotted as squares. In both cells a close correspondence with the area–threshold curves can be seen, except for the large-spot region in Fig. 1(b), indicating the power of the latency method to eliminate even threshold-raising inhibition. Yet only little additional sensitivity is revealed outside the threshold-determined borders of the center. To both cells and both methods a cumulative Gaussian sensitivity distribution with $\sigma = 0.085$ mm gives a good fit. (Note that the description of the RF center by a 45° line and a horizontal line referred to above is intended to stress certain *functional* features—i.a. that the center does, after all, get rather close to performing complete spatial summation. The description by a Gaussian arises from anatomical and physiological considerations—the probable strength of synaptic coupling between receptor and ganglion cell as a function of the distance from the RF midpoint—but any elongation of the receptive field would also show as a slope less than 45° in an area-threshold measurement.) A similar comparison was made in 5 cells with consistent results. We conclude that in most cells no more than a 20% fraction of the total center sensitively may remain outside the (stimulus) area where the horizontal part of the area–threshold curve is first reached. This corresponds to a potential 0.1 log unit sensitivity increase when stimuli extend beyond that area. Normally we had to resort to the area–threshold method of mapping the center, as a good intensity–latency measurement is far too time-consuming.

The occurrence of surround responses

For each cell we first determined the area–threshold function, then looked for the annulus dimensions giving the best surround responses (observing the limitations mentioned in the Methods section) and measured thresholds to it. Table 1 summarizes our findings on the 82 cells examined for cone-mediated surround responses (excluding six aberrant cells; see the last section of the results). We have divided the positive results into three groups according to the severity of the criterion fulfilled (cumulatively, i.e. cells satisfying the strictest criterion appear also under the looser criteria). In the first, either the on- or the off-response to the best annulus had a lower threshold than the corresponding response to the best spot, in the second the annulus threshold was at the most 0.4 log units higher, and in the third group it was no more than 1 log unit higher. (The reasons for choosing these criteria are set forth in the Table Legend.) With the 1 log unit criterion, not all "surround" responses are necessarily genuine, but on the other hand it may give a better indication of the proportion and kinds of cells having a responsive surround (leading to fewer mistaken rejections). The strictest criterion gives a predominance to cells with on-off asymmetry—especially, all off-center cells (class 4) with pure on-surrounds are to be found here.

Antagonism of center and responsive surround

Off-cells have on-surrounds. As seen from Table 1, the majority (7/9) of the class 4 cells studied had a responsive surround. Yet none gave off-, but only on-responses from the surround. Keating and Gaze (1970), using small-spot mapping, do report off-cells with off-surrounds, but admit that they cannot rule out light scatter. We think this is likely to be the explanation as shown by experiments like that in Fig. 2. (See, however, the later section on aberrant cells.) Here we have characterized the spatial sensitivity distributions of (cone-mediated) off and on-responses

Table 1. Summary of the numbers of ganglion cells of the different classes whose responses to annuli satisfied certain sensitivity criteria. For the characterization of cell classes, see the Methods section.

Class of cell	Criterion (log units) 0	0.4	1	Totals
1–2	2	5	17	32
3	8	14	19	35
4	7	7	7	9
Sum	17	26	43	76

The left-hand column gives the number of cells of each class satisfying the most stringent criterion: that the response threshold to the optimal annulus should actually be *lower* than the corresponding threshold to the optimal central spot. The middle column allows the annulus response to have a 0.4 log units higher threshold than that of the best spot. This criterion should, just as the first one, still exclude all false "surround" responses due to accidental stimulation of the center: assuming that 20% of the center sensitivity may be outside the optimal central spot, this spot covers 80% of the center, while an annulus may cover 20% of it. The annulus further throws 6% stray light on the (remaining 80% of the) center, giving a total of less than 26%. The ratio spot excitation/annulus excitation would then be 80/26 = 3.08, giving a log threshold difference of at least 0.49. So, the 0.4 criterion leaves a safe margin. The third column gives all cells where the annulus response is inexplicable by light scatter alone: 6% light scatter yields a ratio spot excitation/annulus excitation = 80/6 = 13.3 or at least a 1.1 log unit threshold difference.

in a class 4 cell by two methods: first by measuring thresholds to spots of various sizes and annuli of various inner diameters, then by small-spot mapping. (As the *inhibitory* surround of class 4 cells is very weak, they offer the best opportunity for studying the *responsive* surround unsuppressed by inhibition. In fact, in the other cell classes no surround responses could be evoked with small peripheral spots.) Both on- and off-responses could actually be elicited by stimulation very far from the center. However, the off-responses from far had a sensitivity so low as to be wholly accountable for by light scatter on to the center, and they were always of the short-latency "center" type (see below). Therefore, we feel sure that they were not real surround responses.

Opponency in on-off-cells. Given four response mechanisms: both on and off in both center and surround, what is the relation between these? To get a general idea, we plotted the degree of on-dominance in the surround as a function of the degree of on-dominance in the center for all the cells satisfying the 1 log unit criterion in Table 1 (Fig. 3). As expected in view of the potentially strong but highly varying lateral *inhibitory* interference with responses to annuli, the points are strongly scattered. Still an inverse relation can be seen: the stronger the central on-dominance, the more off-dominated is the surround. The correlation between center and surround log dominance ratios was statistically significant ($r = -0.46^{**}$ for the on-off-center cells).

Antagonism at stimulation of the same sign. There is not only the sign opponency of center and surround described above, there is also downright center antagonism against the surround. A direct indication of this is the fact that (unless the green rods are stimulated, see below) a central spot, no matter how large, never evokes an on-response from a class 4 cell (i.e. no surround response on combined stimulation of center + surround). That the antagonism is a general rule is shown by the following experiment. We compared thresholds to (1) a (large) stimulus spot, (2) an annulus having the same outer diameter

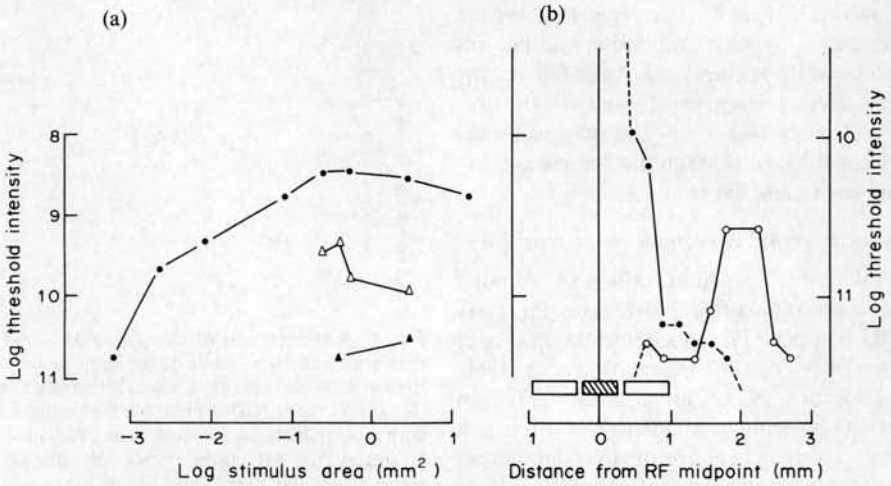

Fig. 2. Thresholds of the *off* and *on* responses of an off-center (class 4) cell when only the cones are stimulated. Thresholds measured (a) with various spots and annuli centered on the RF; (b) with a small spot (0.3 mm dia.) at various distances from the RF center. In (a) the circles signify thresholds to spots and triangles thresholds to annuli; open symbols: on-responses, filled symbols: off-responses; abscissa: log area of stimulating spots or, for annuli, of the dark center. The outer diameter of all annuli was 1.9 mm except for the largest one having 3 mm outer diameter. In (b) the abscissa gives the distance (in mm on the retina) between the RF center and the center of the stimulating spot; the rectangles bottom left show the position and extent of the optimal spot (shaded) and the optimal annulus (open) taken from (a) for comparison. The intensity of the 558 nm background was as usual in (a), but was two log units lower in (b).

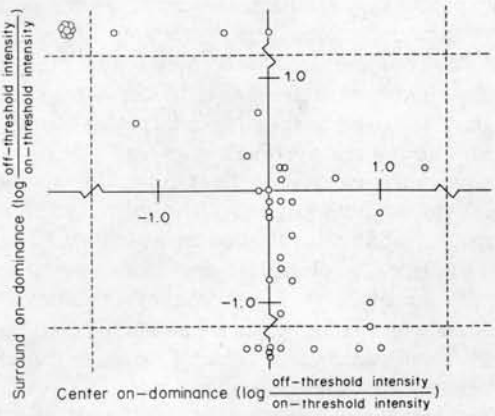

Fig. 3. The degree of on-dominance in the surround plotted as a function of the degree of on-dominance in the center for all the 43 cells with surround responses satisfying the 1 log unit criterion (see Table 1). The axes give the logarithm of the ratio (off-threshold intensity)/(on-threshold intensity) for the center (abscissa) and the surround (ordinate); outside the dashed lines all cells for which these values exceed 1.6 and 1.2 log units respectively are found. (E.G. the raspberry in the upper left-hand corner contains all seven off-center cells with pure on-surrounds.) Excluding the pure off-center, on-surround cells, which might otherwise alone create the impression of significant correlation, we calculated the coefficient of linear correlation (r) between the coordinates of the rest of the points. Assigning the values 1.6 and 1.2 respectively to coordinates falling outside the dashed lines, we obtained the correlation coefficient $r = -0.46$ for the 36 on-off-center cells. This is significant on the 0.01 probability level.

as the spot, and (3) an annulus having the same dimensions as (2), but letting through 10% of the light in the center, i.e. inside its inner border. Typical results are shown in Fig. 4. It emerges that for the responses classified as surround responses, the annulus simultaneously letting weak light fall on the center always gives a lower sensitivity than the normal annulus. The reversal of on- and off-sensitivities in passing from the spot through the "semi-annulus" to the annulus can also be seen.

The responsive surround is not movement-sensitive

In the cat retina ganglion cells can respond strongly to stimulation of retinal regions far away from the RF proper. This phenomenon has been called the periphery or shift effect (McIlwain, 1966; Krüger and Fischer, 1973; Barlow *et al.*, 1977), an excellent stimulus being a sudden shift of e.g. a black-striped grating. There are obvious similarities between the shift effect in cat and surround responses in frog, e.g. both are optimally activated by a sudden change in illumination over a large area and both are accessory effects in cells already endowed with both on and off response mechanisms. Is the frog surround more akin to the shift effect or to the classical cat RF surround? To test this we projected an annulus which, when turned on and off, gave good surround responses as an additional steady (615 nm) background superposed on the usual 558 nm background. Then we moved a black-striped grating (spatial frequency 1.7 cycles/mm on the retina) against this annular background. Whilst the cell always responded vigorously to the introduction or withdrawal of the grating (halving or doubling the light flux), it never responded to a subsequent jerk or movement of the grating in any direction or at any speed (except if the annulus was so narrow in relation to the spatial frequency of the grating that the movement caused a suprathreshold fluctuation of the total light flux). The lack of sensitivity to movement was confirmed also by moving dark spots of various sizes against the annular background. These tests we carried out regularly, in about half of all the cells examined for surround responses, with consistent results. If the background annulus was slightly shifted to illuminate the edge of the RF center, vigorous responses to at least some of the moving stimuli could always be obtained. The unknown amount of inhibition activated by these gratings and spots makes the evidence somewhat less compelling, still the inference is that the responses from the frog surround do not really resemble those due to the shift effect in the cat. This is also indicated by the center-surround antagonism, having no counterpart in the relation between center and shift responses.

Response dynamics

It may seem a perplexing task for a ganglion cell with on-off-center plus antagonistic on-off-surround to produce orderly responses to step stimuli. The signals might even be expected to cancel out.

The fact that central excitatory on- and off-channels (Frumkes and Miller, 1979) as well as

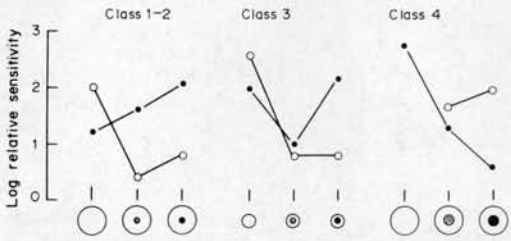

Fig. 4. A comparison of thresholds obtained with a large spot and with two annuli of the same outer diameter: one letting 10% of the light directly through in the center (Kodak Wratten N.D. 1 filter; stippled in the figure) and one with a completely dark center. (The irradiance on the center produced by the three types of stimuli were then, respectively, 100%, 16% and 6% of the nominal intensity.) Examples are shown from one sustained (class 1–2) cell, one class 3 and one class 4 cell (from left to right). Open symbols: on, solid symbols: off. Outer and inner stimulus diameters were 1.9 and 0.3, 0.8 and 0.3, and 1.9 and 0.8 mm in the three cases. According to our usual threshold criteria only the off-responses to annuli in the two first cells and the on-responses in the third cell were judged as true surround responses. The ordinate in this Figure gives only relative sensitivities, as the sensitivities of the three cells differed somewhat and the absolute values are unimportant.

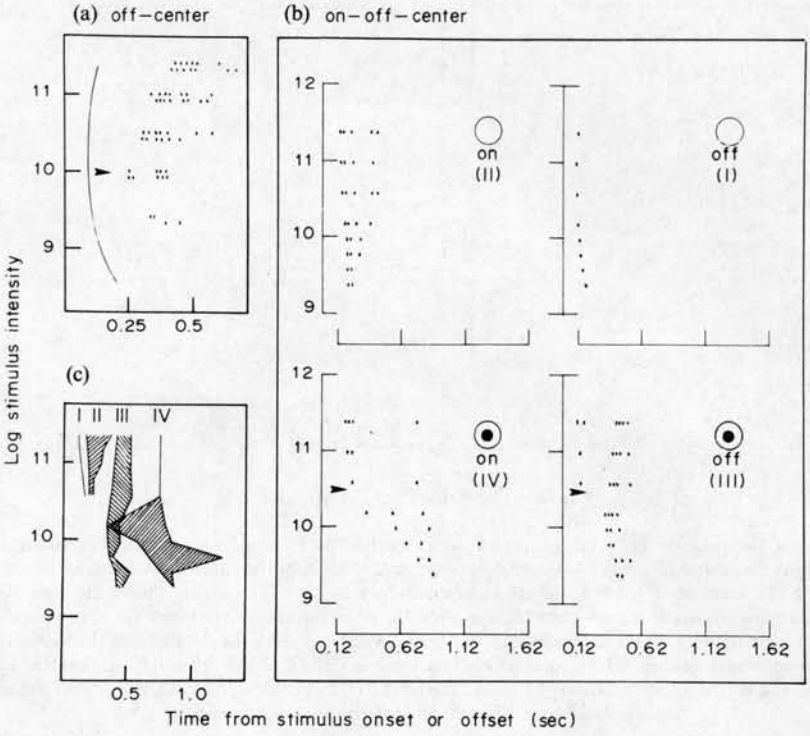

Fig. 5. The dynamics of supra-threshold surround responses compared with center responses in an off-center (class 4) cell (a) and an on-off-center (class 1–2) cell (b) and (c). Each row of dots is an impulse discharge to the stimulus intensity given by the ordinate. The abscissa gives time from the start of stimulation (light on or off at the left edge of each frame). (a): class 4 cell, responses to an annulus (i.d. 0.8 mm, o.d. 1.9 mm) turned on at the left edge. Two responses to each stimulus intensity are shown to give an idea of variability. The curved line gives, for comparison, the latencies of the off-responses obtained when the whole RF center is stimulated with a spot of the respective intensities. (b): class 1–2 cell, responses to spots (1.9 mm dia.) and annuli (i.d. 0.67 mm, o.d. 1.9 mm) turned on (left column) or off (right column) at the time marked by the intensity axis. The arrows in the annulus records show the intensity where, counting with 6% light scatter on to the center, center responses would be expected to start appearing. (c): the time–intensity domains occupied by each of the four response components in (b). *I* signifies center off, *II* center on, *III* surround off and *IV* surround on. For details, see text.

the excitatory and lateral inhibitory pathways (Nye and Naka, 1971; Copenhagen, 1975; Donner, 1981a) have different dynamics makes it reasonable to suspect a temporal segregation of the signals. To investigate this, we recorded series of supra-threshold responses both from the center and the surround, in 0.4 log unit steps from threshold up to the full intensity of our optical system (Fig. 5). Response dynamics are most conveniently first characterized in a class 4 cell [Fig. 5(a)], where one knows that surround on-responses cannot be due to light scatter even at high stimulus intensities and where the responses are little disturbed by inhibition. Naturally, in on-off-center cells supra-threshold responses can only by analogy be ascribed to the surround.

As seen in Fig. 5(a), the latencies of surround responses are quite different from those of center responses over the whole intensity range. Not only are they much longer, their intensity-dependence is also different. In view of the similar properties of the on-off-cell's supra-threshold responses to annuli [Fig. 5(b) III and IV] we shall tentatively call them surround responses as well. Note that, because of light scatter, center-type short-latency responses start appearing at the higher stimulus intensities, weakening the surround component [from the arrowheads upwards in Fig. 5(b), bottom frames].

Figure 5(c) is a schematic presentation of the time-courses of the four response components—center off (I), center on (II), surround off (III) and surround on (IV)—obtained from Fig. 5(b). We have simply connected the first spikes of the responses in each frame of Fig. 5(b) (discounting, however, the fast component above the arrowheads in the responses to annuli), done likewise with the last spikes, and thus obtained for each response component a rough response time as a function of stimulus intensity. Then we have collected all four sets into the same frame, only shifting the center responses 1.2 log units upwards on the intensity scale to simulate the stimulation by 6% light scatter experienced by the center when annular stimuli are used. A picture of almost complete temporal separation of the components emerges. We did such an analysis on five similar cells with on-off-balance in center and surround and the results were essentially consistent.

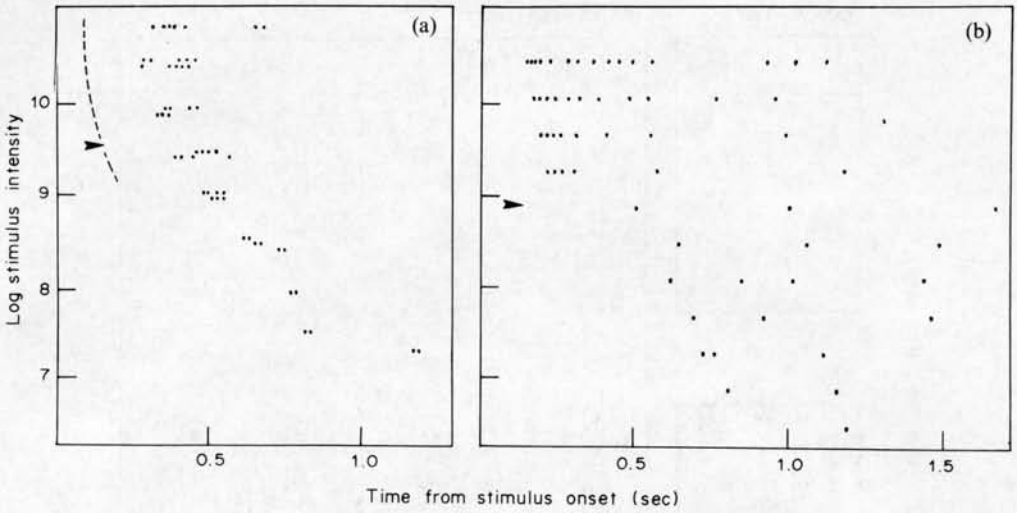

Fig. 6. How the relation between green-rod- and cone-mediated response dynamics is different in the surround (a) and center (b). (a) Shows on-responses recorded from the same class 4 cell as shown in Fig. 5(a), using the same annulus, but 435 nm light instead of 615 nm. The arrow shows the cone-threshold for the 435 nm annulus, inferred from the observed threshold to the 615 nm annulus on the basis of the cone spectral sensitivity function (see legend to Fig. 7). As in Fig. 5(a), the dashed line shows the latencies of central off-responses. (b) On-responses evoked from a class 1–2 cell by a 435 nm central spot (dia 0.53 mm). The arrow again indicates the cone-threshold to the 435 nm spot, calculated from the observed threshold to a 615 nm spot of the same dimensions.

Spectral properties

Receptor input. The results presented so far all refer to a situation where only the cones are stimulated. However, we also studied 13 fully dark-adapted cells at near-threshold intensities, where only the red rods are active. Unambiguous surround responses were found in 9 of these (0.4 log unit criterion): class 1–2 (1/3), class 3 (4/5) and class 4 (4/5). This established two things: (1) the RF retains its organization also with respect to the responsive surround when switching from cones to red rods; (2) the responsive surround does not disappear even on complete dark-adaptation. The differences in dynamics between center and surround responses were likewise similar to those seen under cone stimulation.

The green rods are a different matter altogether. Although more than half of the light-adapted cells we investigated did have a green rod input, we were never able by stimulation of the green rods to elicit an annulus response which could not be attributed to illumination of the large green-rod-mediated "center" and response dynamics were similar for spot and annulus stimulation. The latter point, that dynamically surround and green rod responses form a population distinct from cone center responses, is clearly borne out by Fig. 6. It displays two sets of discharge patterns evoked by turning on a 435 nm annulus (a) and spot (b). In the surround [Fig. 6(a)] there is a smooth transition from green-rod- to cone-mediated responses as stimulus intensity is raised, whilst in the center responses [Fig. 6(b)] there is a clear discontinuity at the intensity where the cones begin to intrude. This is interesting, bearing in mind that besides having large RFs and long latencies, green rod responses resemble surround responses in yet a third respect (Reuter and Virtanen, 1972): in class 4 cells, where central cones respond only to *off*, they are *on*-responses.

Spectral sensitivity of center and surround. Reuter and Virtanen (1972) have previously shown that the spectral sensitivity of the photopic center under a strong yellow-green background closely follows two curves: (1) that describing the combined cone sensitivity of the frog ($\lambda_{max} = 560$ nm) and, if there is input from the green rods, (2) the absorption spectrum of the green rod pigment ($\lambda_{max} = 433$ nm). Accordingly, the different relation between cone and green rod signals in the center and surround would be expected to produce differing spectral sensitivities. Figure 7 shows spectral sensitivity functions recorded from the center and the surround of three cells: one where the center was pure *off* (a–b), one *on-off*-balanced (c–d) and one with an *on*-dominated center (e–f). The cone and green rod receptor curves have been drawn into all the figures to serve as a reference to which the observed sensitivities can be related.

We did find systematic differences between center and surround, most readily appreciated from the relatively simple situation in a class 4 cell [consider Fig. 7(a) vs 7(b)]. In the center [Fig. 7(b)] the cones give only off-responses, the green rods only on-responses, and the latter are completely suppressed in the wavelength region where the former are more sensitive. As we move into the surround [Fig. 7(a)], the cone signal reverses sign from *off* to *on*, but the green rod signal remains *on*. As a consequence, the

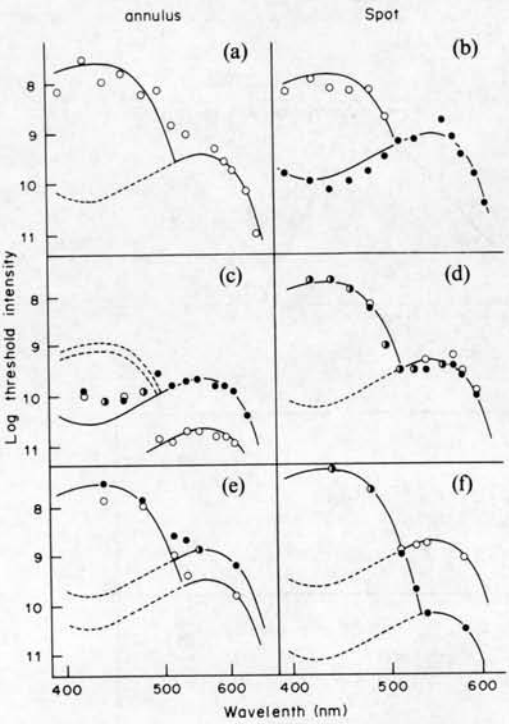

Fig. 7. Spectral sensitivity functions from the periphery (left column) and the center (right column) of the receptive fields of three ganglion cells. We have selected one cell which, when only cones were stimulated, showed a pure off-center (class 4, a–b), one with on-off-balance in the center (class 3, c–d) and one with an on-dominated center (class 3, e–f). The thresholds to stimulation with lights of different wavelengths were measured using annuli for stimulation in the left column and a central 0.3 mm spot in the right column [dimensions in (a): i.d. 0.8, 2.5; (c): i.d. 0.3, 0.8; (e): i.d. 0.53, 1.9 mm]. The 558 nm background was the usual $3 \cdot 10^{10}$ quanta $\cdot sec^{-1} \cdot mm^{-2}$ in a–b and e–f, but in c–d it was ten times higher. The curves are: (1) peaking at 433 nm, the absorption spectrum of the visual pigment of the green rods (Dartnall, 1967, recalculated for an optic density maximum of 0.3 in accordance with the shorter outer segments of the green rods); (2) peaking at 560 nm, the combined cone sensitivity of the frog (Granit, 1942; Reuter, 1969). The curves have been vertically placed by eye to give best fit to the points in the short-wavelength region (the 433 nm curve) and the long-wavelength region (the 615 nm curve) respectively.

two signals become synergic and there is summation in the region of equal sensitivity (i.e. around the point where the curves intersect). A similar positive deviation from receptor sensitivity curves around the point of intersection is to be seen in the surrounds of the on-off-cells as well [Fig. 7(c) and (e)], but not in their centers [Fig. 7(d) and (f)]. Still more remarkable deviations were observed in "aberrant" cells (see Fig. 9). We recorded spectral sensitivity functions from both the center and the surround of ten cells and in the surrounds of seven there was constructive interaction between receptors, making the sensitivities deviate significantly from "pure" receptor sensitivity curves.

We cannot rule out the possibility that the red rods, in spite of the saturating background, play some part in the surround's spectral sensitivity, but the deviations from the cone and green rod curves persisted even when the background intensity was elevated by one more log unit. The unknown role of the double cone containing a pigment peaking at 502 nm further complicates the interpretation.

Surround responses are not a rebound effect

The following experiments employing disinhibitory drugs were carried out because we wanted to know whether there is a distinct cellular pathway mediating surround excitation. It could be argued that surround responses arise as a form of rebound excitation upon the termination of an inhibitory signal; then they would be just a curious side-effect of lateral inhibition seen under unnatural stimulus conditions.

Speaking against that argument is the fact that surround responses are especially strong in cells virtually lacking lateral inhibition (class 4) and are rarest in strongly inhibited cells (class 1–2; cf. Table 1). Our idea was to establish this artificially by blocking inhibitory pathways with the GABA- and glycine-antagonists picrotoxin and strychnine. The drugs were injected into the eyecup as described in the Methods section; thus administered they have been found to suppress lateral inhibition in the same preparation as we were using (Bäckström, 1981; Grönholm and Reuter, 1981).

The weakening of inhibition can be seen either as a sensitization of the responses or, at supra-threshold stimulation, as an increase in their number of impulses. We used both to monitor the effects of the drugs. Under the rebound excitation hypothesis the following effects on surround responses would be expected from suppressing inhibition: (1) thresholds ought to rise and (2) the impulse discharges of supra-threshold responses get weaker and their latencies shorten to the point of confluence with the strengthened, scatter-induced center responses. We tested seven cells with picrotoxin and seven with strychnine (full intensity–response series were recorded in only three of each). The expected effects were observed in none save one picrotoxin-treated cell where the surround responses disappeared. On the other hand, opposite effects were found in five of both the picrotoxin and the strychine cells. Figure 8 shows examples of these effects on thresholds [Fig. 8(a–b)] and discharge patterns [Fig. 8(c)] recorded from one strychnine-treated and one picrotoxin-treated cell. In Fig. 8(a) strychnine not only sensitized annulus responses, it also brought out previously unseen on-responses to spots and off-responses to annuli. In the strongly inhibited cell of Fig. 8(b–c), picrotoxin unveiled surround responses as well as responses to large spots. But, most important [Fig. 8(c)], the impulse discharges to supra-threshold stimulation with annuli revealed no tendency to dissolve into "center" responses, but remained a dynamically entirely distinct population.

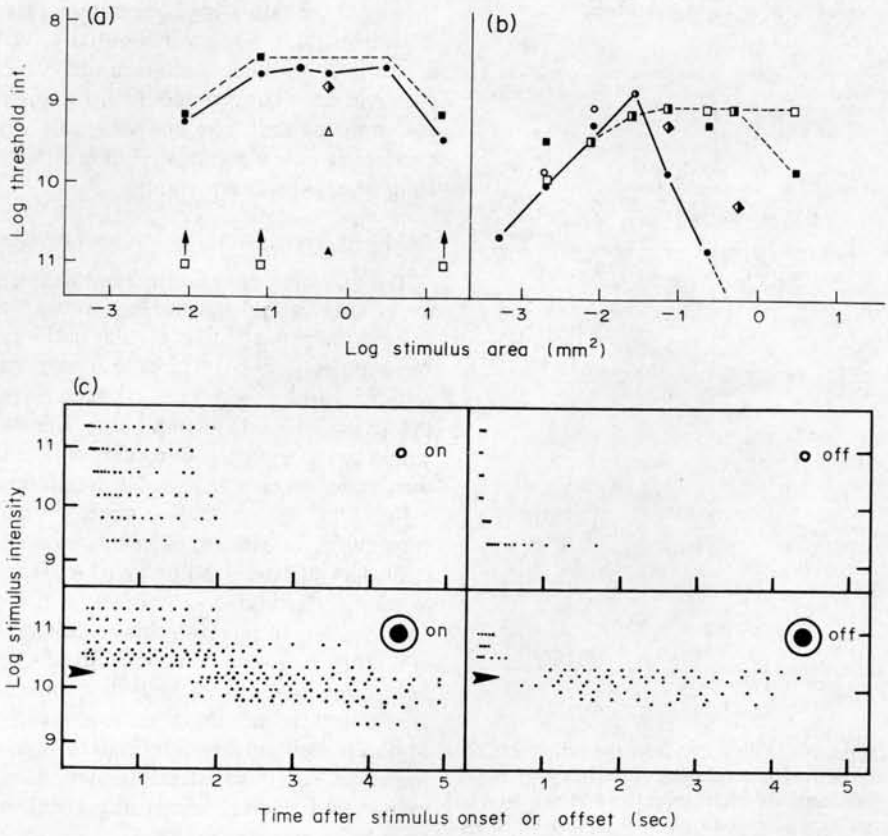

Fig. 8. Effects of strychnine (a) and picrotoxin, (b) and (c), on thresholds and discharge patterns of center and surround responses. (a) and (b) display area-threshold functions plus thresholds to annuli before and after the application of the respective drug. Explanation of symbols: circles—spot thresholds before drug application, squares—spot thresholds after drug application, triangles—annulus thresholds before drug, diamonds—annulus thresholds after drug. Open symbols: on, solid symbols: off. Abscissae give spot area and, for annuli, the area of the dark center, the outer diameter being 1.9 mm except for the lower diamond in (b), where the outer diameter was 3 mm. The cell in (a) was, before strychnine, pure off-center, on-surround, but behaved more like a class 3 than a class 4 cell (possibly a "deviating class 4" according to Bäckström and Reuter 1975); strychnine brought out a central on-reponse as well as a surround-off. Unfortunately we lost the cell before we could determine precise central on-thresholds. (c) Discharge patterns recorded from the cell shown in (b) about 1 h after the application of picrotoxin. Responses to a small (0.11 mm dia) centrally placed spot (top frames) and an annulus (i.d. 0.3, o.d. 1.9 mm; bottom frames) turned on (left column) and off (right column). The responses are displayed in the same manner as in Figs 5 and 6. The arrows connected with the responses to annuli indicate the intensity where, according to 6% light scatter, center responses would be expected to start appearing. We recorded responses at denser-than-usual intensity intervals around this transition zone to ascertain that the responses latency-wise fell into two distinct populations. Note that the very long latencies of 2 sec or more in the annulus responses are due to the inherent slowness of surround responses and, probably, to center antagonism. They are not examples of the delayed afterdischarges (Pickering and Varjú, 1969; Chino and Sturr, 1975), which occur only in the dark-adapted eye and, under step stimulation, only after off. The latencies of those discharges grow as stimulus intensity is raised, up to even 90 sec at high intensities (Donner, unpublished).

Cells giving surround-type responses to central spots

Among the 82 cells investigated for cone-mediated surrounds we found six aberrant cells surprisingly combining in their responses to centrally placed spots turned on and off three characteristics of *surround* responses: (1) a wide-spread sensitivity distribution with no antagonistic surround. In one case [Fig. 9(a)] the RF covered the whole retina when explored with the area-threshold method, but when stimulated with dark spots moving on a background, even this cell gave brisk responses from an area corresponding to a normal-sized RF center (0.3 mm diam.). (2) A surround-type intensity-latency function. (3) A spectral sensitivity function that showed an occasionally dramatic deviation from all "pure" receptor sensitivity curves [Fig. 9(b)]. A natural interpretation would be that in these cells only a surround-type pathway is activated by on-off-stimuli, while the normal center-type pathway is reserved for movement detection.

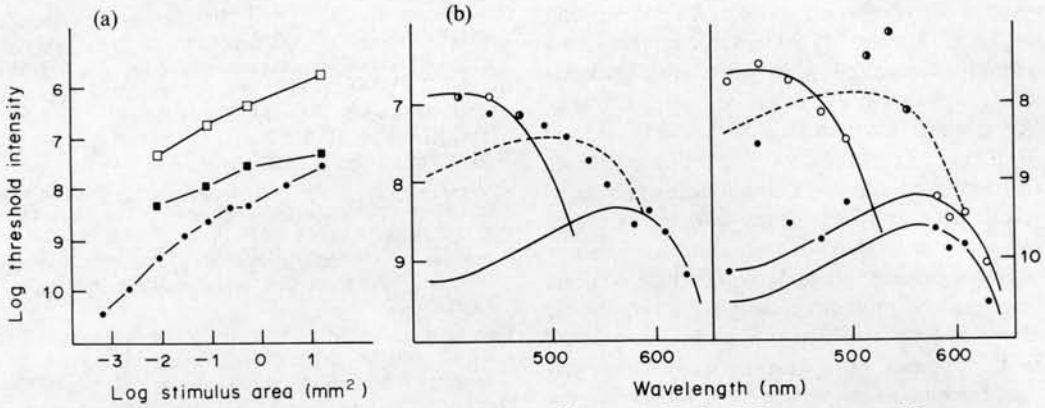

Fig. 9. (a) Area-threshold functions from an aberrant cell (see text). Circles: 615 nm, squares: 435 nm; open symbols: on, solid symbols: off. (b) Spectral sensitivities of two similar cells (stimulus centrally placed spot 0.3 mm dia). In addition to the curves defined in the legend to Fig. 7, the absorption spectrum of frog rhodopsin (Dartnall 1953, recalculated for an optical density maximum of 0.5 cf. Donner and Reuter 1965) has been drawn as a dashed line to illustrate that no single receptor sensitivities, nor mere cone-red-rod-summation, can account for the observed ganglion cell sensitivities. The 558 nm background was as usual in (a) and the left part of (b), but was 10 times stronger in the right part of (b).

DISCUSSION

Comparison with other vertebrates

We have found a responsive surround to be a common feature of the ganglion cell classes 1–4 of the frog retina. Considering the ubiquity of antagonistic, not purely inhibitory, surrounds in the RF organization of vertebrates, both lower (fish) and higher (reptiles, birds, mammals; for a review see e.g. Rodieck, 1973), this only amounts to filling in what has seemed rather a surprising gap. (The on and off response mechanisms of the frog RF center only occasionally show a partial spatial separation and they are not really center-surround-organized (Barlow, 1953; Zhukov, 1980).) However, a novel feature in comparison with other vertebrates is that, on stimulation of one single receptor type, cells endowed with both an on and off response mechanism in the center may also give both on and off responses from the surround. This is different from all known cases of a similar degree of complexity–both from double colour opponency and from the cat's shift effect.

Further these experiments demonstrate that two different types of lateral interactions can be physiologically distinguished at the ganglion cell level: antagonistic and purely suppressive ones. Figure 10 is intended as an updating of Grüsser's and Grüsser-Cornehls' (1973) much-reproduced schematic representation of the frog ganglion call RF in terms of spatial sensitivity distributions. Three basic functional components are distinguished and by different weighting of these, different RFs can be assembled. The occurrence of an excitatory surround pathway is probably more common than shown by our extracellular recordings, where that signal is seen only if it overcomes both inhibition and center antagonism.

Cellular basis

All normal cone- or red-rod-mediated RF centers

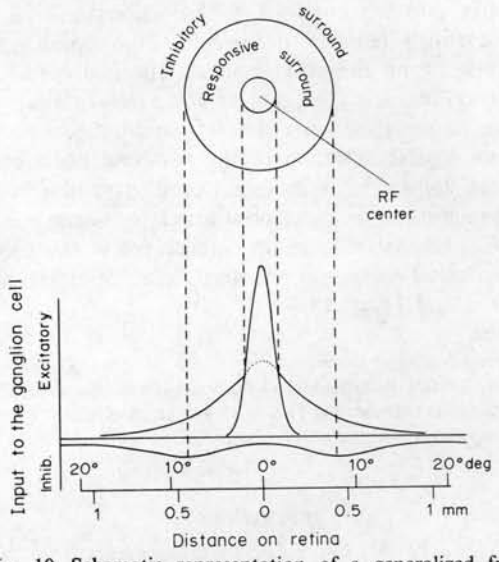

Fig. 10. Schematic representation of a generalized frog ganglion cell RF in terms of spatial sensitivity distributions. The excitatory *center* mechanism has been drawn as a Gaussian following Grüsser and Grüsser-Cornehls (1973) and our Fig. 1. The *representative radius* of the center is that which, if the sensitivity distribution were a top-hat function with peak sensitivity equal to that of the Gaussian, would contain the integrated sensitivity. The exact profile of the excitatory *surround* mechanism cannot be inferred from experiments such as that in Fig. 2, because it is always distorted by center antagonism. Instead, we have hypothesized a near-exponential fall-off towards the periphery justified by the general similarity of surround responses and green-rod-mediated responses. The latter, at least sometimes, reveal an exponentially falling distribution (cf. Bäckström and Reuter, 1975). Under the center it may be Gaussian, but we have no experimental evidence. Finally, the *inhibitory* mechanism(s) are represented by a distribution peaking at some distance from the borders of the center, but falling again towards the RF midpoint. This is based on direct measurements by Bäckström and Reuter (1982), which give good reason to reject the Gaussian favoured by Grüsser and Grüsser-Cornehls (1973). All mechanisms overlap and the crude map displayed above the sensitivity profiles only expresses which mechanism is the dominant one in each area.

encountered by us and others (e.g. Bäckström and Reuter, 1975; Donner, 1981b) in the frog have had a size entirely compatible with histologically determined ganglion cell dendritic trees (range 0.03–0.6 mm dia. according to Kock, Mecke, Reuter and Wallgren, in preparation). For center responses it is then sufficient, although by no means necessary, to hypothesize a straight pathway from the receptors through bipolars to ganglion cells. But many of our surround responses originated at quite distant points on the retina and must necessarily have been transmitted by at least one extra interneuron. And all surround responses show features supporting that idea, i.e. the change of sign and the longer latency compared with the center.

It seems natural to interpret the surround responses as a consequence of the center-surround organization of the bipolars (Matsumoto and Naka, 1972; Yang *et al.*, 1983). Under this interpretation, the antagonism between two "excitatory" signals—center and surround—is to be understood as a competition between two signals of opposite sign impinging on the same bipolar. The two kinds of lateral influences (antagonistic and purely inhibitory) seen at the ganglion cell level would then be the physiological reflection of the two-level horizontal processing in the retina—the former resulting from interactions in the outer plexiform layer (Yang *et al.*, 1983), the latter based on connections in the inner plexiform (Werblin and Copenhagen, 1974; Marchiafava and Torre, 1978).

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