

GANGLION CELL RESPONSE CHARACTERISTICS FROM THE AREA CENTRALIS IN  
THE INTACT EYE OF THE CAT

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**ARMY - NAVY**

**Joint Report**



U. S. ARMY AEROMEDICAL RESEARCH UNIT

NAVAL AEROSPACE MEDICAL INSTITUTE

February 1968

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Unclassified

Security Classification

DOCUMENT CONTROL DATA - R & D

(Security classification of title, body of abstract and indexing annotation must be entered when the overall report is classified)

1. ORIGINATING ACTIVITY (Corporate author)  Naval Aerospace Medical Institute Pensacola, Florida 32512		2a. REPORT SECURITY CLASSIFICATION  Unclassified	
		2b. GROUP  N/A	
3. REPORT TITLE  GANGLION CELL RESPONSE CHARACTERISTICS FROM THE AREA CENTRALIS IN THE INTACT EYE OF THE CAT			
4. DESCRIPTIVE NOTES (Type of report and inclusive dates)			
5. AUTHOR(S) (First name, middle initial, last name)  Captain Roy H. Steinberg, USAR, MC			
6. REPORT DATE  14 February 1968		7a. TOTAL NO. OF PAGES  42	7b. NO. OF REFS  33
8a. CONTRACT OR GRANT NO.		9a. ORIGINATOR'S REPORT NUMBER(S)  NAMI-1031	
b. PROJECT NO. MR005.04-0088.2		9b. OTHER REPORT NO(S) (Any other numbers that may be assigned this report)  USAARU Serial No. 68-5	
c.			
d.			
10. DISTRIBUTION STATEMENT  This document has been approved for public release and sale; its distribution is unlimited.			
11. SUPPLEMENTARY NOTES  Joint report with U. S. Army Aeromedical Research Unit, Fort Rucker, Alabama		12. SPONSORING MILITARY ACTIVITY	
13. ABSTRACT  Ganglion cell responses were recorded with microelectrodes from the intact eye to focused spots and annuli of light delivered by a dual-beam ophthalmoscope. Only concentrically organized circular receptive fields were analysed. Thresholds for optimal center and surround stimuli were approximately equal, as were the latencies of on-responses from the center and surround. With whole-field stimulation center-dominance was a function of light intensity. Off-responses and center-surround interaction were observed with brief flashes (5 msec, 10 msec). With increases of flash duration the duration of the on-response did not increase by the full increment of the flash until the flashes were 50 to 80 msec. At high-flash intensities the on-response extended into the off-period and the off-response weakened and disappeared; it occurred with both on-excitation and on-inhibition and for the responses of both center and surround. These intensity effects were also studied in an intracellular recording; at high intensities, the rate of re-polarization of the postsynaptic potential decreased, and the latency of repolarization was delayed.			

14. KEY WORDS	LINK A		LINK B		LINK C	
	ROLE	WT	ROLE	WT	ROLE	WT
Ganglion cell						
Receptive field						
Retina						
Local electroretinogram						
Afterimage						

## SUMMARY PAGE

### THE PROBLEM

The purpose of the present investigation was to describe the response characteristics of ganglion cells from the area centralis.

### FINDINGS

#### Part I

(1) As determined by an area-threshold technique, the majority of circular receptive field-diameters were  $> 1.5$  mm, while 40 per cent were smaller (0.80 mm to 1.50 mm). Field centers ranged from 0.125 mm to 0.80 mm in diameter and the majority were  $\leq 0.33$  mm in diameter. (2) The area-threshold functions for the center and surround of each field varied considerably and in two fields crossed at the points of optimal threshold. (3) The threshold intensities of flashes that optimally stimulated the surround or center were equal (45 per cent) or nearly equal. (Mean difference in threshold, 0.23 log unit.) (4) Area-threshold analyses were difficult to accomplish with brief flashes (5 msec, 10 msec). When they could be done, center-surround interaction, as evidenced by a rise in threshold, was still observed. (5) The latencies of the on-response evoked by optimal center and surround stimuli were not significantly different. (6) In response to stimulation of the entire receptive field (whole field) at low-flash intensities ( $\leq 1.0$  log unit above threshold) surround responses were often observed in combination with center responses (on-off responses). At higher intensities, however, only the center response was observed (center-dominance). (7) Center-type responses were occasionally observed at the edge of the receptive field at low intensities of the flash. (8) With optimal stimulation of the surround the effects of stray light were usually first observed at 1.5 to 2.5 log units above threshold. (9) The on- and off-response both were observed in response to brief flashes. (10) As flash duration was increased, the duration of the on-response did not increase by the full increment of the flash until the flashes were 50 to 80 msec in duration. (11) The strength of the off-response was enhanced by increasing the duration of the flash up to about 250 msec. (12) With whole-field stimulation the center-surround interaction that occurred with brief flashes was not significantly different from the interaction that occurred with longer flashes.

#### Part II

(1) At relatively high intensities of the flash ( $> 2.0$  log units above threshold) the on-response extended into the off-period. The duration of the extension increased approximately as a linear function of log intensity. At the same time the latency of the off-response increased, and with additional elevations of flash intensity the off-response weakened and disappeared. (2) This phenomenon occurred with both on-excitation and on-inhibition and for the responses of both center and surround. (3) It

was observed for all of the flash durations between 5 msec and 1.0 sec. (4) At high-flash intensities a remnant of the off-response often persisted at a short latency while the main portion of the off-response increased in latency. This discontinuity of the off-response usually occurred at relatively long durations of the flash (e.g., 500 msec). At the highest intensities of the flash the short-latency remnant also weakened and disappeared. (5) These intensity effects were also studied in an intracellular recording. At high intensities the rate of repolarization of the PSP decreased and its latency was delayed.

#### ACKNOWLEDGMENTS

Michael L. Walker and Scott Morrill provided technical assistance through all phases of this work.

## INTRODUCTION

The response characteristics of the d.c. component of the local electroretinogram, recorded in the area centralis of the cat retina, were recently described (1). The behavior of this component with alterations in the area, intensity, and duration of the stimulus, combined with the probability of an origin in the inner nuclear layer, suggested that it may be directly involved in the generation of ganglion cell activity. If this is so, then the response characteristics of ganglion cells in the area centralis should be compatible with those of the slow potential. The present investigation was undertaken, therefore, in order to describe the behavior of area centralis ganglion cells under the stimulus conditions of the earlier study.

Ganglion cell activity in the area centralis of cat has been previously recorded (2-7). Receptive fields in this area are generally similar to those of the peripheral retina as they are predominantly circular and exhibit a concentric center-surround organization, although a significant number of specialized fields have been reported (6, 7). The anatomy of the ganglion cell layer of the area centralis has also been described in recent anatomical studies (8, 9). A high cellular density ( $\geq 3000/\text{mm}^2$ ) and the small size of the cell bodies (80 per cent  $< 15\mu$ ) are its most significant features relative to the peripheral retina.

This report describes the response characteristics of only those ganglion cells that exhibited concentrically organized circular receptive fields, since they were the type most often encountered and were easily studied with conventional techniques of stimulation, i.e., flashing spots and annuli of light. It will be shown that the responses of ganglion cells and the behavior of the d.c. component of the local electroretinogram are significantly similar. In particular, a counterpart for the high-intensity effect, delay of decay of the d.c. component, appeared in a ganglion cell event, extension of the on-response. In addition, while studying response alterations that accompanied small changes in the parameters of the stimulus, a number of observations were made regarding the spatial organization of the receptive field, the properties of the center and surround, and of center-surround interaction. The report is divided, therefore, into two parts. Part I describes the response properties of these cells with alterations in the conditions of stimulation, particularly with regard to center-surround organization, while Part II describes the extension of the on-response.

## PROCEDURE

A detailed description of the methods that were used in these experiments was presented in a previous report (1).

The results were derived from an analysis of the responses of 91 cells in 22 cats. All of the action potentials were recorded with glass microelectrodes (3M-KCl) which penetrated the surface of the retina at the area centralis. Difficulties were not encountered in recording the activity of individual cells in this area of the retina as had

been reported by other investigators (6). In fact, action spikes from single ganglion cells were obtained on more than 50 per cent of the penetrations. The amplitudes of the extracellular action potentials were usually 0.5 mV to 3.0 mV, and higher voltages were often observed (3.0 mV to 14.0 mV). A concentric location of the receptive field, in the immediate vicinity of the microelectrode tip, identified cellular recordings in contrast to axonal ones.

Only those cells that exhibited circular receptive fields, organized into concentric center and surround areas, were included in this analysis. Other types of fields were rarely encountered, probably because of limitations in the method of stimulating the retina, i.e., flashing spots and annuli of light (6, 7).

An area-threshold technique was employed to identify the borders of the circular receptive fields (4, 10, 11). A background beam provided a constant level of light adaptation within the recording area of 0.45 to 45 lumens/m<sup>2</sup>. A small spot of light (diameter, 0.057 mm or 0.083 mm) was flashed in the vicinity of the microelectrode tip in order to identify the type of center response [on-excitation or on-inhibition, corresponding to the on-center, off-center classification of Kuffler (2)] and to locate the point of maximum response and lowest threshold. The threshold was defined subjectively by the intensity of flashes which evoked a visible or audible change in the spontaneous level of activity at least 50 per cent of the time. It could usually be assessed to within  $\pm 0.1$  log unit. After locating the most sensitive point, the flashing spot (170 msec to 500 msec in duration; repeated every 10 to 30 sec) was enlarged in fixed steps, and the threshold intensity of each spot was determined. (The diameter of these spots on the retina was: 0.057, 0.083, 0.125, 0.17, 0.33, 0.50, 0.67, 0.84, 1.00, 1.17, 1.34, 1.57, 1.67, 1.84, 2.00 mm.) The optimal stimulus, in area and location, for the receptive-field center was defined by the diameter of the spot that produced a threshold response at the lowest intensity of the flash. A similar analysis was performed with annular shaped flashes having a fixed outer diameter (usually 2.00 mm). The area of the annulus was increased by decreasing the inner diameter in fixed steps. The optimal stimulus for the surround was defined by the inner and outer diameters of the annulus that produced a threshold response at the lowest intensity of the flash. Thresholds for the optimal center and surround stimuli were repeatedly checked throughout the experiment.

All of the data were recorded on magnetic tape (Ampex FR-1800L tape recorder) after amplification in a conventional manner. For photography, the brightness of the action potentials was enhanced relative to the brightness of the baseline by modulating the Z-axis (Tektronix 565 oscilloscope) with a pulse from a waveform generator (Tektronix 161) that had been triggered by a pulse which was derived from the action potential. This system is responsible for the discontinuity in the spikes that appears in some of the illustrations.

## PART I: RESULTS

### AREA-THRESHOLD ANALYSIS

#### Size of Receptive Fields

Complete area-threshold analyses were performed on 41 cells in 12 cats. The results of this analysis agree, in general, with those obtained by Wiesel (4) in the lightly anesthetized cat. He found that the receptive-field centers of cells in the area centralis were smaller than those in the periphery; i.e., the majority of center-diameters in the area centralis were  $< 0.25$  mm; while in the present study the majority of receptive-field centers summed within an area  $0.33$  mm in diameter. A moderate number of larger centers were observed, however, (35 per cent summed within an area  $0.33$  mm to  $0.80$  mm in diameter), while the smallest center had a diameter of only  $0.125$  mm [in agreement with the value obtained by other investigators (4, 6, 12, 13)].\*

The values for the total diameters of the receptive fields observed in the present study agreed, again, with those obtained by Wiesel ( $1.5$  to  $3.0$  mm). However, a significant number (40 per cent) of smaller fields, i.e.,  $< 1.5$  mm in diameter ( $0.80$  mm to  $1.50$  mm), were also identified.

The threshold intensities of the optimal surround stimulus (an annulus) and the optimal center stimulus (a spot) were usually quite close in any one field. Actually, in 45 per cent of the fields the thresholds of these optimal stimuli were equal ( $\pm 0.1$  log unit). Even when the thresholds differed (45 per cent center  $<$  surround; 10 per cent surround  $<$  center), the difference was small (mean difference,  $0.23$  log unit; range,  $0.1$  to  $0.5$ ; S.D.,  $0.15$ ).

Figure 1 presents the area-threshold curves from three cells; each curve was selected to illustrate a particular feature of the analysis. In (A), both the center and surround functions are approximately symmetrical. Increasing the diameter of the centered spot brought the threshold of the center response to a minimum (the optimal center stimulus); additional enlargement of the spot then elevated the threshold. In the total population of cells enlargement of the spot to the optimum reduced the threshold by an average of  $1.10$  log units (range,  $0.5$  to  $1.9$ ; S.D.,  $0.3$ ); further enlargement to the edge of the field elevated the threshold by  $0.5$  log unit (range,  $0.0$  to  $0.9$ ; S.D.,  $0.15$ ). Figure 1(A) also illustrates the change in threshold of the surround response when the area of the annulus was increased by decreasing its inner diameter. (Enlargement of the annulus is read from right to left since the abscissa now indicates the area of the inner diameter.) The optimum inner diameter of the surround

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\*Stone and Fabian (6) used averaged-response histograms and described a class of specialized receptive fields in the area centralis of the cat that were characterized by small centers ( $0.091$  mm to  $0.125$  mm; mean,  $0.10$  mm). However, centers that were  $< 0.125$  mm in diameter were not identified by the area-threshold technique in the present investigation.

stimulus almost always coincided with the optimum diameter of the center stimulus. Enlargement of the annulus first lowered the threshold until the optimum was reached (mean, 1.0 log unit; range 0.3 to 2.4; S.D., 0.16), while further enlargement elevated the threshold (mean, 0.4 log unit; range 0.0 to 0.9; S.D., 0.20). Some fields had an intermediate zone in which the thresholds of the center and surround responses stayed near the minimum level [Figure 1(B)]. In other fields, inclusion of the antagonistic area had little or no effect on the threshold [Figure 1(C), center]. The three graphs of Figure 1 illustrate the tendency for the optimal center and surround thresholds to be equal.

In the field illustrated in Figure 1(B), the thresholds of the optimal center and surround stimuli actually were equal, while in Figure 1(C) the threshold of the surround was lower than that of the center. Figure 1(C) also illustrates a rare finding (2 cells), i.e., a crossing of the optimal points of the center and surround; consequently, in these fields the optimal areas for each mechanism overlapped.

Threshold determinations with flashes < 20 msec in duration were complicated by a tendency to confuse center and surround responses. For example, a 10-msec flash to the center, when the response was on-excitation, evoked a weak burst of action spikes at a long latency. A flash to the surround, at threshold, also evoked a long-latency burst of spikes (the off-response) which was not easily distinguished from the on-response of the center. It was especially difficult with brief flashes (5 msec, 10 msec), therefore, to define the limits of the center and surround areas and to follow the threshold of each response beyond its optimal point. In a few cases, however, this analysis could be performed since the center and surround responses clearly differed (e.g., based on an obvious difference in the latency of the center and surround bursts or the identification of one of the mechanisms by its inhibitory period). In Figure 2, for example, the area-threshold functions for center responses to 5 msec and 500 msec flashes are compared. Although the thresholds at 5 msec were elevated (1.1 log units at the optimal point), and the function was somewhat flatter at both ends, the shape of the two functions was almost identical and inclusion of the surround area elevated the threshold of the center response in both cases.

## FLASH INTENSITY

### Latencies of Center and Surround Responses

The relatively greater distance of the optimal surround area from the ganglion cell, in comparison to the center, suggests that surround responses should occur at longer latencies than center responses. Problems arise, however, in choosing the latencies which are to be compared. For example, in each receptive field, a comparison of the latencies of the on- or off-responses of the opposing receptive field mechanisms requires that the latency of an inhibitory response be compared with the latency of an excitatory response; but measurement of the latency of inhibition is usually less precise than that of excitation. On the other hand, a comparison of the

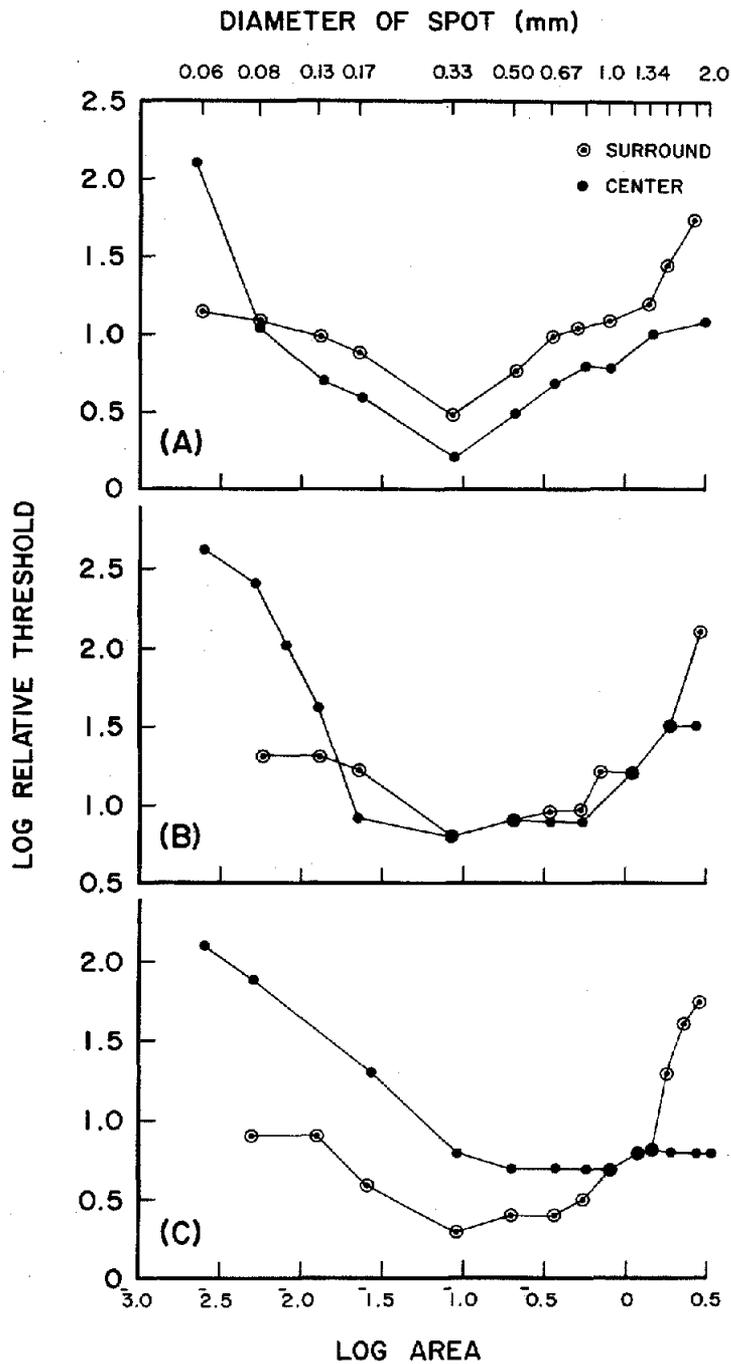


Figure 1

Area-threshold curves for both center and surround responses in three different ganglion cells. Abcissa: Center responses-- $\log_{10}$  area of the spot. The diameters of the spots, in millimeters, are also indicated at the top of the graph. Surround--the inner diameter of the annular stimulus. Ordinate: threshold, relative  $\log_{10}$  scale.  $\circ$  equals a retinal illuminance of  $0.45 \text{ lumens/m}^2$ . Level of adapting illuminance,  $45 \text{ lumens/m}^2$ . Flash duration, 250 msec. Center responses: (A), on-excitation, (B) and (C), on-inhibition.

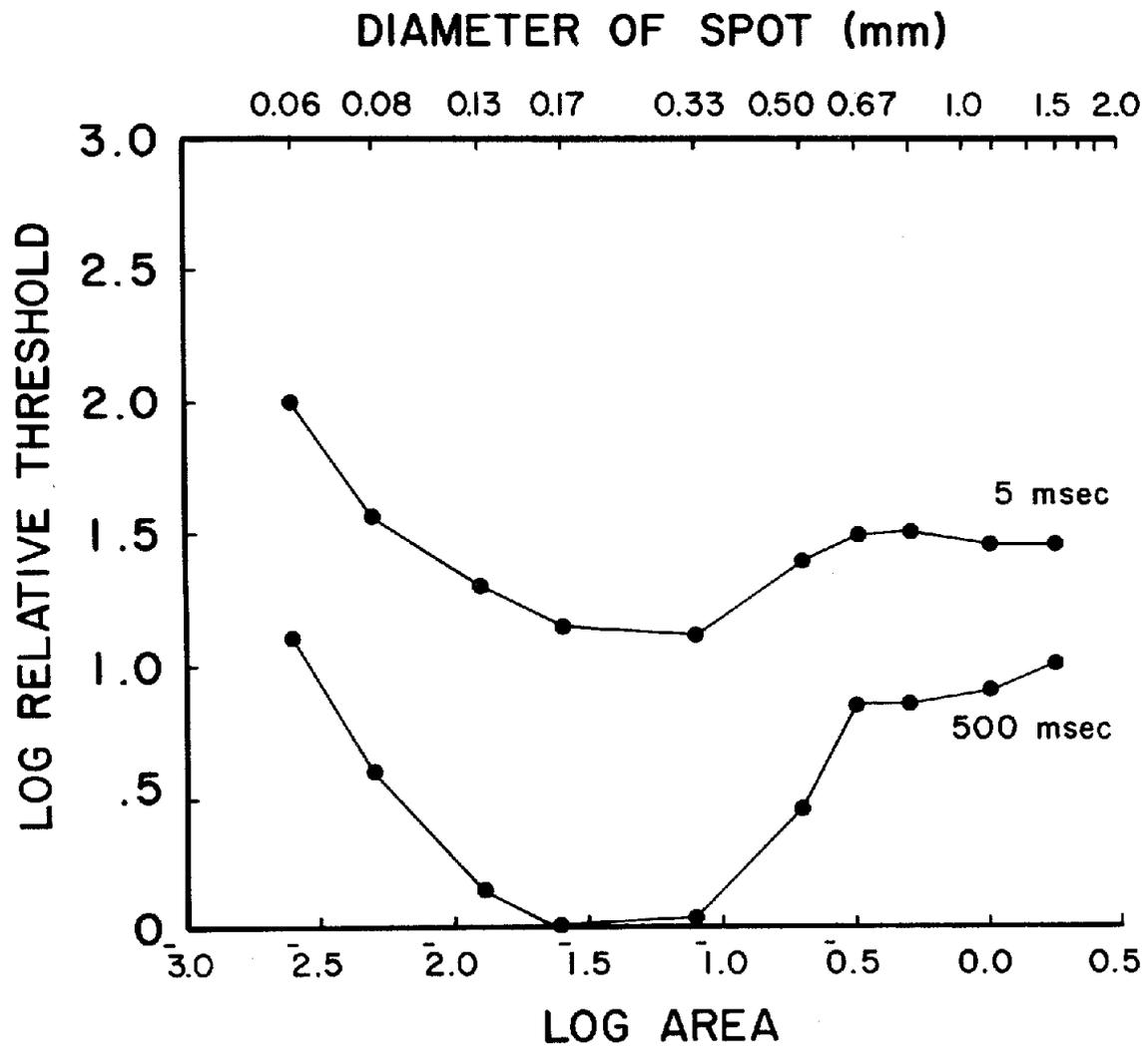


Figure 2

Area-threshold curves at two different durations of the flash (5 msec, 500 msec) for center responses in one ganglion cell. Center response was on-excitation. Otherwise as Figure 1.

latencies of responses of the same sign in any one field requires that on-responses be compared with off-responses, but the on- and off-mechanisms may not be equivalent in this respect. Throughout the population of ganglion cells, therefore, the easiest and most reliable comparisons seemed to be between the latencies of center and surround on-excitation, followed by the comparison of like-signed off-responses. The stimuli were chosen to optimally stimulate each receptive-field mechanism and to produce, thereby, responses at minimum latencies. Response latencies were compared for stimuli of 500 msec to 1000 msec duration, and 0.8 to 1.8 log units above threshold. (The shortest latencies occurred at 1.0 to 1.6 log units above threshold.) With 200 measurements made in 14 ganglion cells the difference between the latencies of the center and surround on-responses was not significant (mean--center, 21 msec; surround, 23 msec.) Similarly the latencies of off-inhibition did not differ significantly. There was a trend for off-excitation from the surround to occur at a longer latency than off-excitation from the center (35 msec vs 20 msec).

### Interaction Between Center and Surround

An increase in the intensity of a flash to either the optimal surround or center area produced the anticipated enhancement of response latency, discharge frequency, and duration (2). The response to a combined center and surround stimulus (whole-field stimulation) also showed these effects, and an examination of the discharge patterns, through a range of intensities, revealed that the responses were altered in a specific way. At low intensities stimulation of the entire receptive field often produced a weak on-off pattern (excitation at both on and off), while at higher intensities the response consisted of only the on-excitation or on-inhibition response pattern. In effect, at relatively low intensities (0.1 to 1.0 log unit above threshold) the response of the ganglion cell was clearly formed by a combination of the center and surround responses. At higher intensity levels the response was dominated by one of the mechanisms, almost always the center.

Figure 3 shows the responses of a cell to flashes that stimulated the center, the surround, and the entire receptive field through a 2.0 log unit range of intensities.\* Increasing the intensity of a small spot (0.33 mm diameter) enhanced the on-inhibition and off-excitation that were distinctive of the center. Similarly, elevations in intensity strengthened the surround response (on-excitation, off-inhibition) when it was stimulated. In response to whole-field stimulation, however, both on- and off-excitation can be observed at low intensities. In fact, in this unit the center and surround responses were both present at the lowest intensity at which a response could be recognized. Increasing the intensity slightly enhanced the surround response (on-excitation), as evidenced by an increase in the number of spikes and shortening in latency of the on-response (0.6 log unit); and the center response (off-excitation)

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\*Grouped discharges (14) were more often observed in response to stimulation of the whole field than with isolated stimulation of either the surround or center. For example, in the ganglion cell of Figure 3, they can be observed in response to whole-field stimulation at 2.0 log units.

was also enhanced. Above 0.6 log unit the center response progressively dominated the discharge pattern, and at 2.0 only the center-response pattern could be identified.

In other receptive fields the surround response was not observed, with whole-field stimulation, at any intensity. In these cells, however, the antagonistic influence of the surround was often indicated by a relative failure of the center-dominated response to enhance with an initial increase in intensity of about 1.0 log unit. For example, in one on-center field (not illustrated) the frequency of the on-discharge was unchanged, despite an increase in flash intensity of 0.6 log unit. It can be assumed that the lack of enhancement signified a concurrent increase in the strength of on-inhibition from the surround.

This effect of intensity on the response of ganglion cells also occurred when the stimulus was located in an area of the receptive field that substantially activated both mechanisms, typically at the "intermediate" area (2). Figure 4 presents a ganglion cell's responses to four annular shaped flashes that were placed at different locations in its receptive field. The smallest annulus, A, was located within the center and the response (on-excitation, off-inhibition) was strengthened by increasing the flash intensity (0.8, 1.8). In B, the annulus was located in an area that gave on-off excitatory responses, indicating that both mechanisms had been excited; although the center mechanism ultimately dominated the response since it was enhanced, relative to the surround, at higher intensities. Note that at low (0.4) and moderate (0.8) intensities the off-excitation (surround) and on-excitation (center) were approximately equal in strength (discharge frequency). In this area, therefore, the center and surround mechanisms overlapped considerably but center-dominance occurred at high intensities. An annulus placed somewhat more peripherally, C, however, produced responses that were characteristic of the surround at all intensities.

In several fields, center-type responses were observed at low intensities at the edge of the surround area, well beyond the area where the surround mechanism had dominated the response. This phenomenon is illustrated in D of Figure 4 where on-excitation, which must have originated from the center mechanism, occurred at low intensities (0.8 log unit). At higher intensities (1.8 log units) surround-dominance was established. The center mechanism could not have been triggered by stray light falling within the center area because the effect appeared at low intensities, relative to threshold, where stray light has never been a problem in light-adapted fields. Stray-light stimulation of the surround, however, was identified in this unit at higher intensities.

### Stray-Light Effects

In the majority of experiments the adapting intensity was kept relatively high (4.5 lumens/m<sup>2</sup> to 45.0 lumens/m<sup>2</sup>) in order to eliminate the effects of stray light.

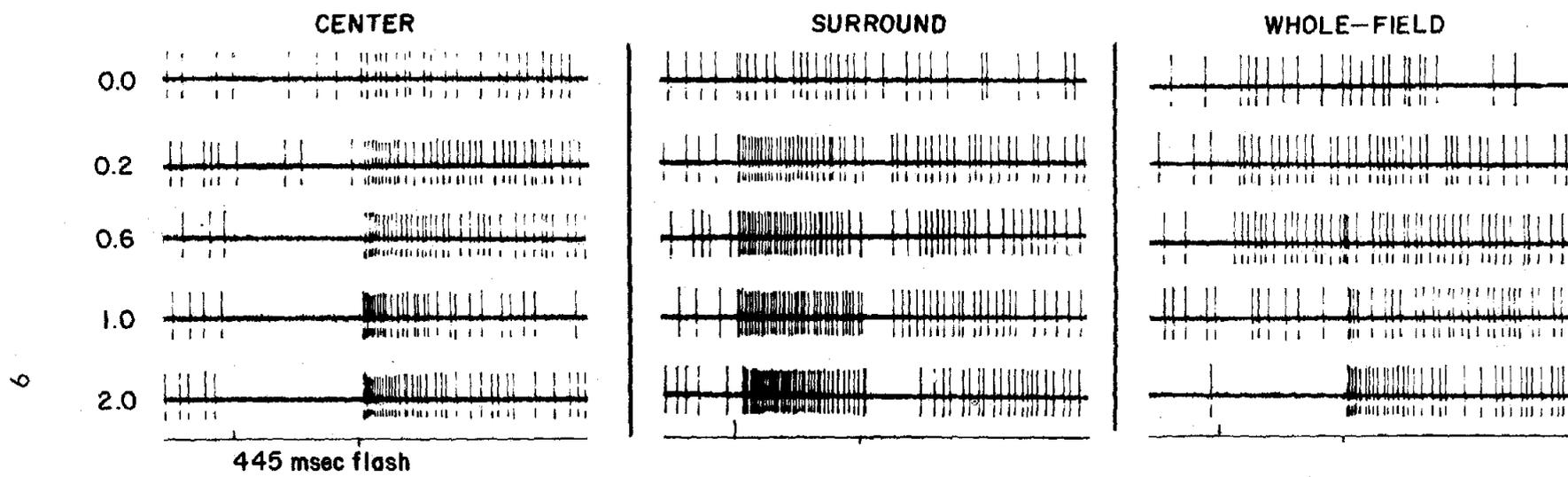


Figure 3

A ganglion cell's response to optimal surround, center, and whole-field stimulation at increasing intensities. Intensities for each response are indicated in the left-hand margin in  $\log_{10}$  units above threshold. Thresholds for both the optimal center and surround stimuli were  $2.8 \text{ lumens/m}^2$ . Adapting intensity,  $45 \text{ lumens/m}^2$ ; flash duration, 445 msec. Diameter of optimal spot, 0.33 mm; optimal surround--inner diameter, 0.33 mm, outer diameter, 1.50 mm. Action spikes were 2.0 mV in amplitude during whole-field illumination. Negative responses are displayed upward, in this and all subsequent figures, unless otherwise indicated.

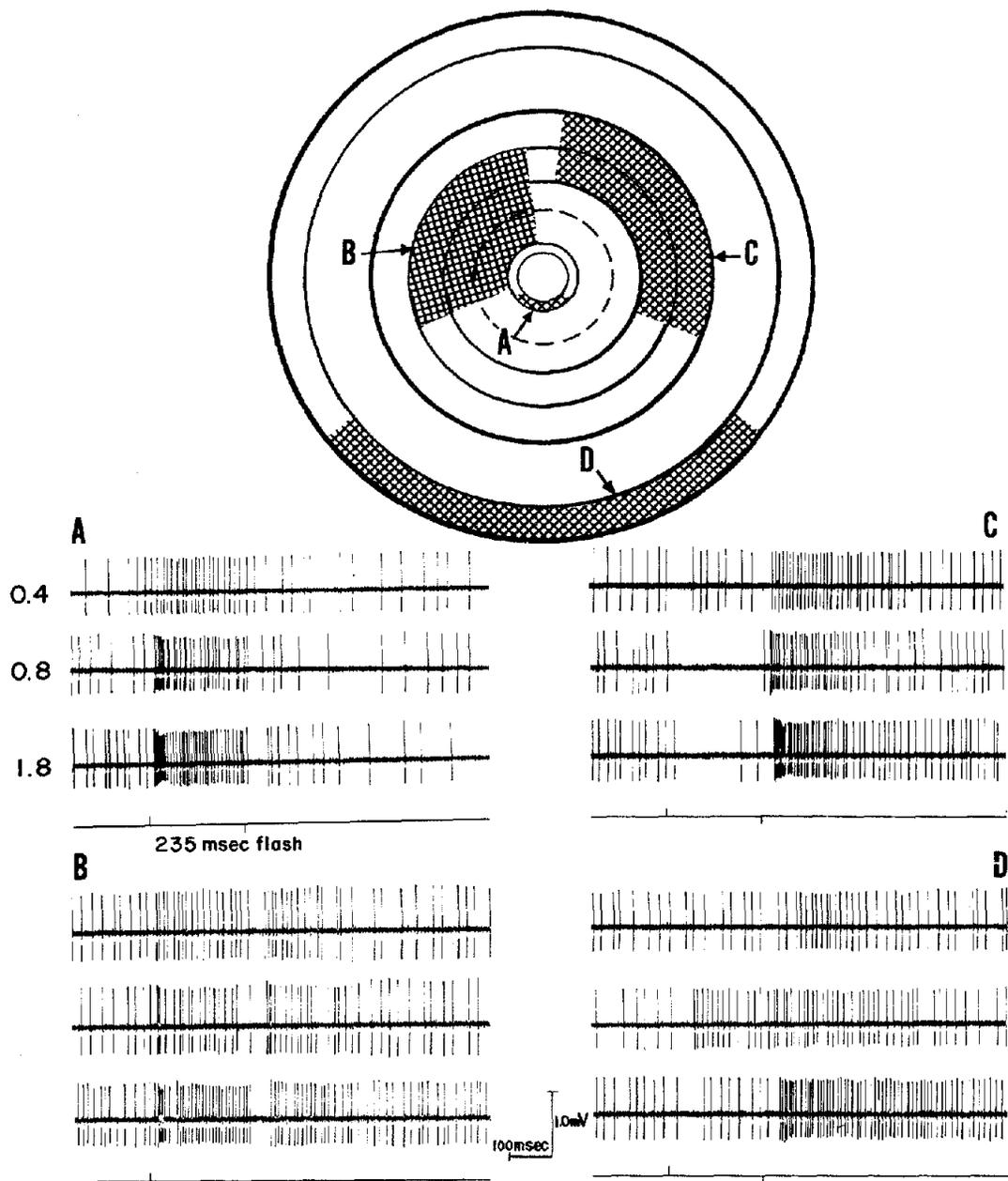


Figure 4

A ganglion cell's response to annular flashes at different loci within its receptive field. The diagram at the top was drawn to a scale of 1:100. The dotted line indicates the boundary of the optimal center stimulus (0.33 mm diameter). The solid lines represent the inner and outer diameters of each annular stimulus, and the area of each stimulus has been partially shaded. The outer diameter of the optimal surround stimulus was 1.34 mm (it is the outer diameter of D). The center response was on-excitation. Flash duration, 235 msec; adapting intensity, 45 lumens/m<sup>2</sup>. Below, the responses to flashes of increasing intensity (0.4, 0.8, 1.8 log<sub>10</sub> units above threshold) are presented for each annulus (A-D).

Ganglion cell response patterns did not differ significantly within this range, but in recent experiments at a lower adapting intensity (0.45 lumens/m<sup>2</sup>), the responses were stronger.\*

Stray-light activation of the surround, with spots spatially located in the center, was never observed. However, annular stimuli within the surround at high intensities invariably excited the center mechanism. These effects began at 1.5 to 2.5 log units above the threshold of the surround response. The consequences of stray light are illustrated, for one field, in Figure 5. At both durations of the flash, the center response (off-excitation) was first evoked at about 1.5 log units above threshold. At higher intensities the off-excitation strengthened (higher frequency and longer duration) and on-inhibition from the center also became prominent (445 msec, 3.0).

This figure illustrates, in addition, that center off-excitation (50 msec series) was actually imposed upon the last impulses of surround on-excitation. For example, the off-excitation initially appeared as a doublet (1.4) or triplet (1.8). Note that despite the onset of center off-excitation, off-inhibition from the surround was still observed. Similarly, in other fields off-inhibition evoked by stray light falling on the center was appended to the on-inhibition of the surround.

## FLASH DURATION

### Off-Response

Brief flashes (5 msec and 10 msec) evoked responses that were always characteristic of the area of the receptive field that had been stimulated. In addition to on-responses, it was usually possible to identify off-responses from both the center and surround. For example, Figure 6 illustrates the response of a unit to optimal surround stimulation with 10 msec flashes. At 0.4 log unit above the threshold of the on-response, an off-response (off-inhibition) could be identified. The off-inhibition was enhanced, as evidenced by a decrease in latency and increase in duration, at higher intensities. At flash durations greater than 10 msec this inhibitory period was also observed, of course, and could then be positively identified as an off-response (Figure 7, surround, duration of 100 msec; from the same cell as Figure 6).

In general, off-responses were always observed, at low intensities, with brief flashes. However, the threshold for identification of the off-response was usually 0.2 to 0.4 log unit above the threshold of the on-response. At longer durations of the flash both thresholds fell, but the threshold of the on-response reached a minimum at relatively short flash durations (50 msec to 70 msec). [Within the 10 msec to 50 msec range, intensity and duration were approximately equivalent (Bunsen-Roscoe law).] The off-response threshold became equal to the on-response threshold only at

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\*In 6 ganglion cells, the mean increment threshold ( $\Delta I/I$ ) was 0.04 (range: 0.02 to 0.08) at an adapting intensity ( $I$ ) of 45 lumens/m<sup>2</sup>. Lowering the adapting intensity 2.0 log units raised the increment threshold to 0.10.

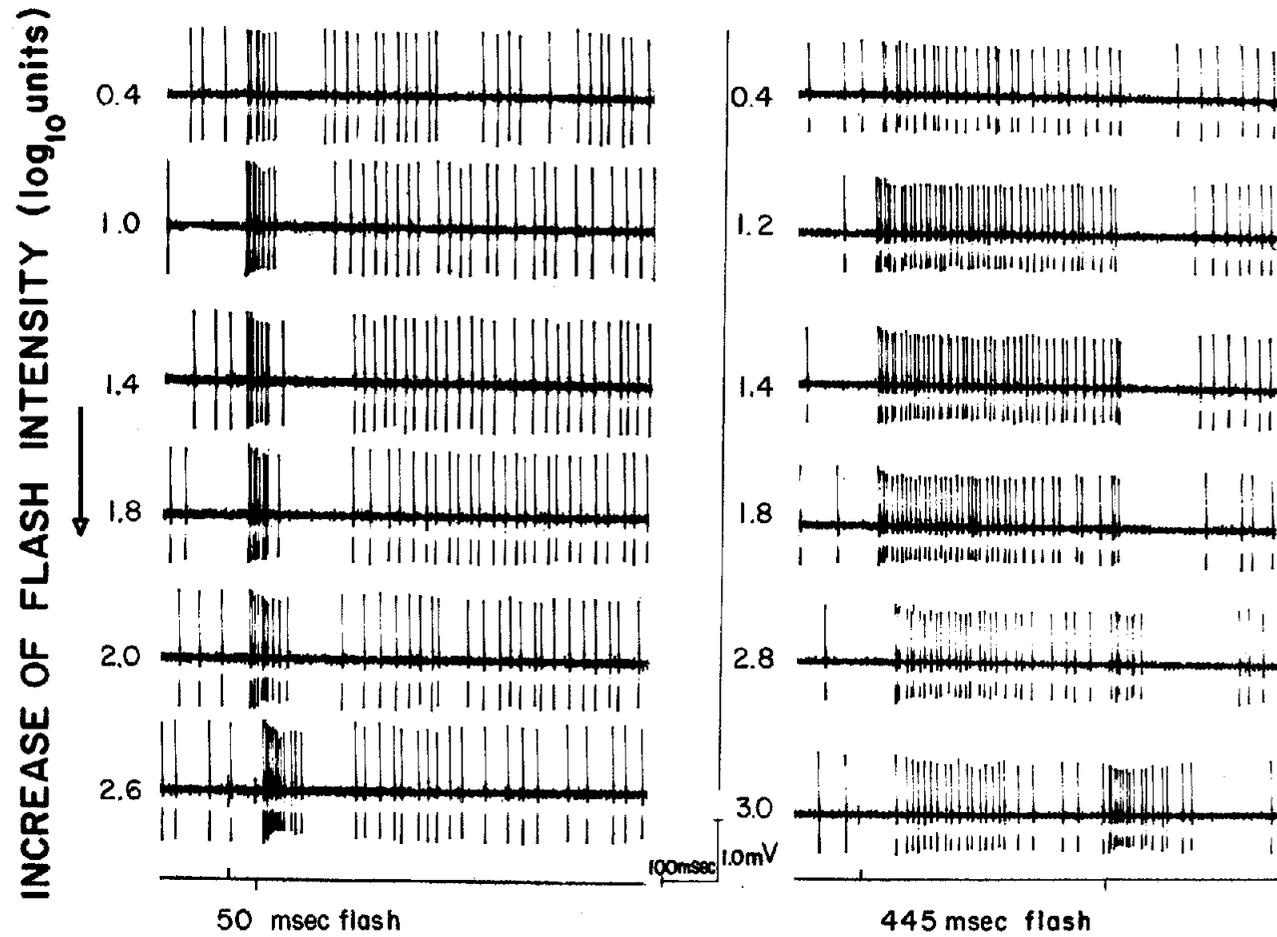


Figure 5

Stray-light effect with surround stimulation at two durations of the flash (50 msec and 445 msec). Optimal surround stimulus--inner diameter, 0.33 mm; outer diameter, 1.50 mm; adapting intensity, 45 lumens/m<sup>2</sup>. The threshold for the 445 msec flash was 1.4 lumens/m<sup>2</sup>.

# INCREASE OF FLASH INTENSITY ( $\log_{10}$ units)

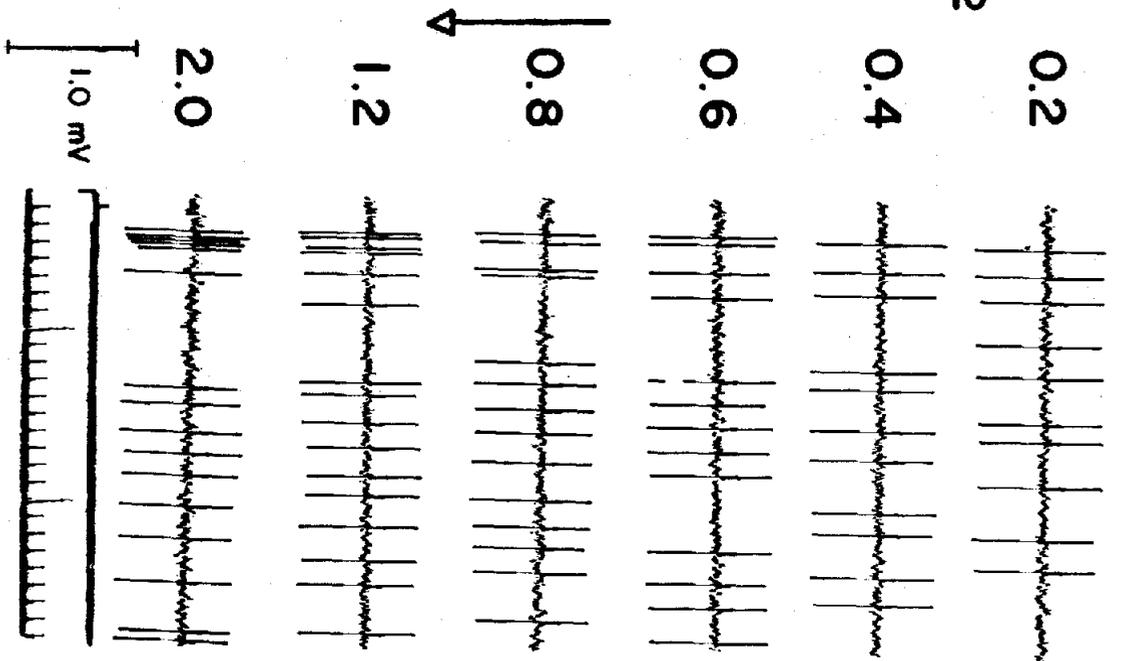


Figure 6

Surround responses to a brief flash (10 msec). Threshold, 45 lumens/m<sup>2</sup>; adapting intensity, 45 lumens/m<sup>2</sup>. Optimal surround stimulus—inner diameter, 0.84 mm; outer diameter, 2.00 mm. Time marks—10 msec and 100 msec.

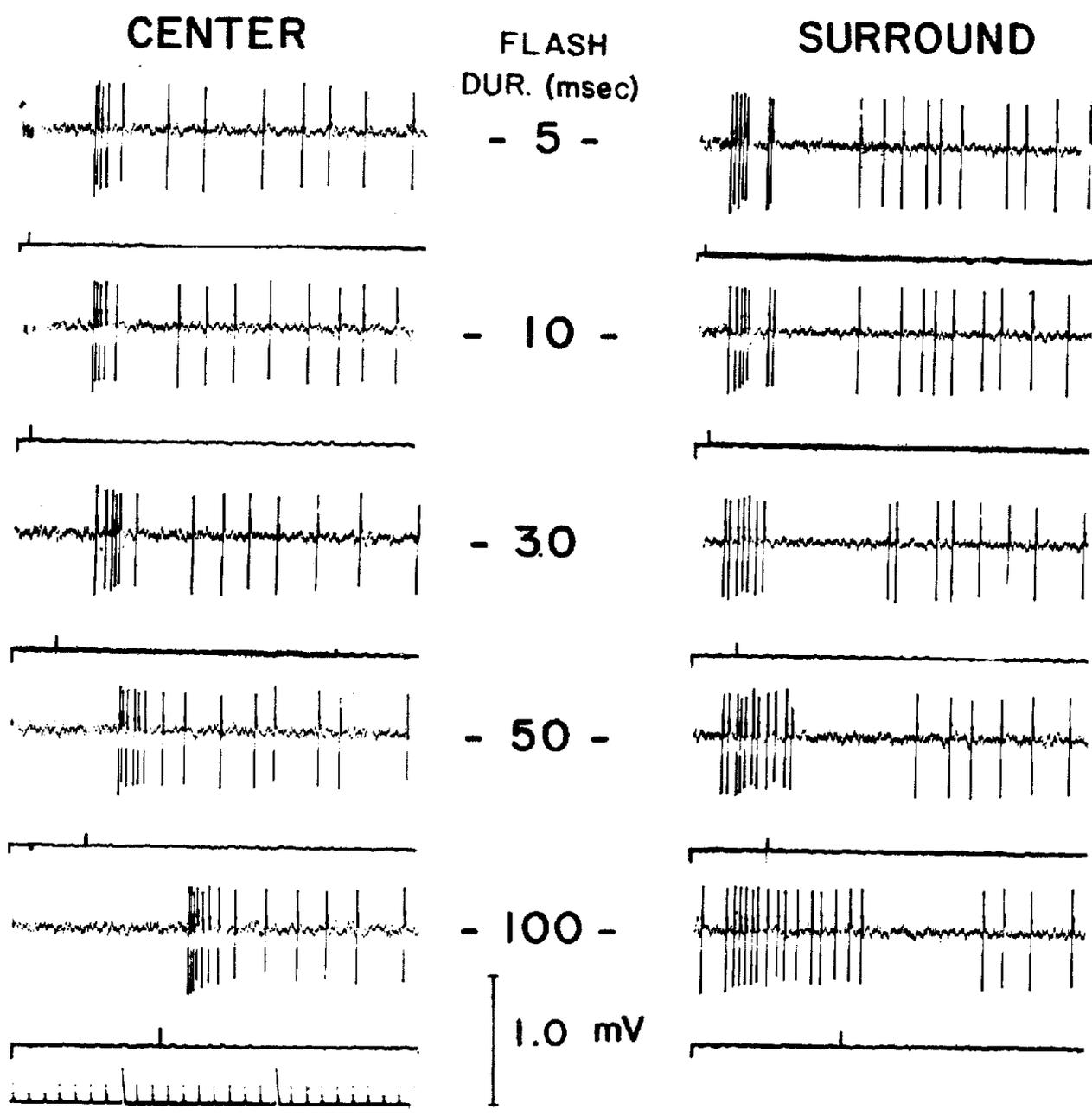


Figure 7

Center and surround responses to flashes of increasing duration from one ganglion cell (the same cell as in Figure 6). Optimal center stimulus, 0.84 mm; optimal surround stimulus--inner diameter, 0.84 mm; outer diameter, 2.00 mm. The flash was 1.6 log<sub>10</sub> units above threshold at each duration. Time marks--10 msec and 100 msec.

flash durations of 250 msec and longer, since the off-response threshold continued to fall as flash duration was increased beyond 50 to 70 msec. This facilitatory effect of flash duration on the off-response was also observed when flash intensity was held constant at a moderate level (1.0 log unit above threshold); then an increase in flash duration (50 to 250 msec) increased the frequency of the response but only slightly shortened its latency.

At brief durations of the flash off-responses occurred at relatively long latencies from the "off" of the flash (e. g., > 50 msec). Increasing the flash duration (5 to 100 msec) reduced the latency of the off-response from the "off" of the flash until it reached a near-minimum value at flash durations of 50 to 80 msec. Figure 7 illustrates this effect for both the center and surround responses of one cell. In both sequences the intensity was above the level which produced a minimum latency of the off-response for each duration of the flash (1.6 log units above threshold). The minimum latency decreased as flash duration was increased until a flash duration of 50 to 80 msec. Beyond this point the off-latency decreased only very slightly or not at all, and the duration of the on-response now increased by the full increment of the flash. In the 5 to 80 msec range, however, the on-response had not increased by the full increment of the flash as the off-response latency fell.

#### Interaction Between Center and Surround

With whole-field stimulation and brief flashes the on- and off-responses of both the center and surround could be identified. The interaction of the center and surround mechanisms did not differ from the interaction described for longer flashes. For example, in Figure 8 the response to a 445 msec whole-field flash (1.4 log units above the threshold of the center response) reflected the activation of both the center and surround mechanisms (center, on-excitation and surround, off-excitation). Both excitatory responses, however, were reduced when compared with the responses obtained at the same intensity with optimal center and surround stimulation. Similarly, the whole-field response to a 10 msec flash (1.2 log units above the threshold of the center mechanism) reflected the activation of both mechanisms. Here, the on-excitation was shortened and the off-excitation reduced in frequency compared with the responses to the optimal center and surround stimuli.

### PART I: DISCUSSION

#### CENTER-SURROUND ORGANIZATION

##### Interaction With Brief Flashes

In enumerating the properties of lateral inhibition exhibited by receptive fields in the cat retina, Barlow et al. (11) included a failure to appear with brief flashes (7 msec in their study) based on area-threshold analyses where threshold elevations were not observed. The data presented above contradict this conclusion by showing that the center and surround mechanisms influence the ganglion cell antagonistically

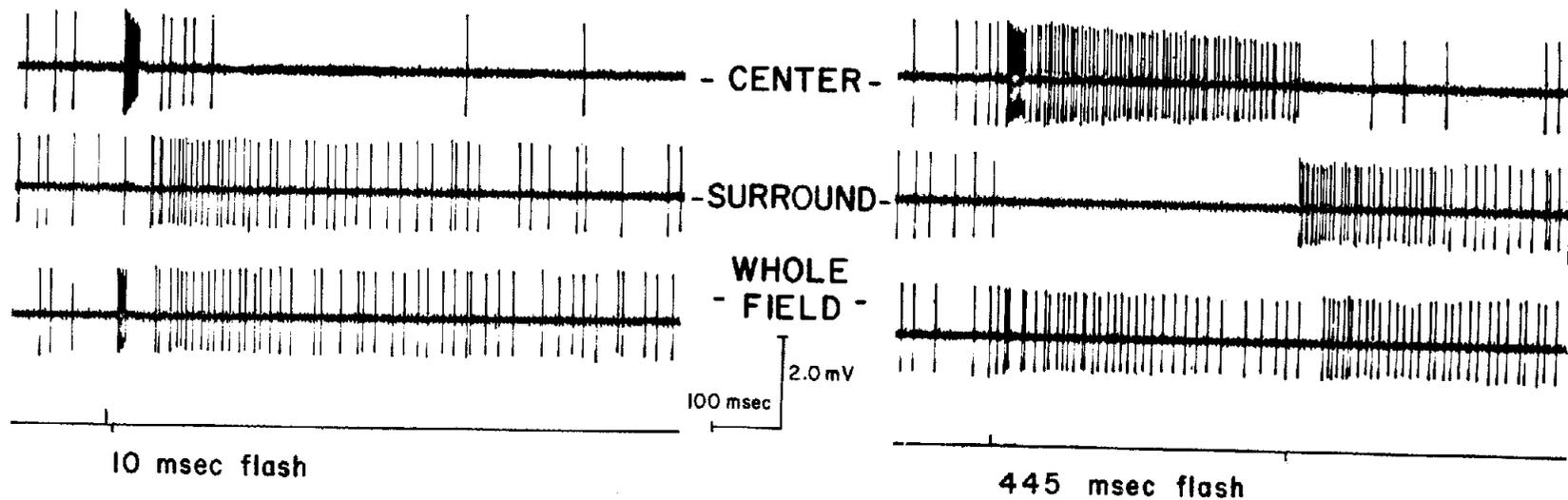


Figure 8

A ganglion cell's response to optimal surround, center, and whole-field stimulation at two durations of the flash (10 msec, 445 msec). Flash intensity was constant in each series (10 msec,  $1.2 \log_{10}$  units above threshold for the optimal center response; 445 msec,  $1.4 \log_{10}$  units above threshold for the optimal center response). Adapting intensity,  $45 \text{ lumens/m}^2$ . Optimal center stimulus, 0.33 mm in diameter; optimal surround stimulus--inner diameter, 0.33 mm; outer diameter, 1.50 mm.

at brief-flash durations (5 msec, 10 msec). The evidence is of two kinds. First of all, and despite the difficulty in performing area-threshold analyses with brief flashes, threshold elevations still occurred when the stimulus overlapped both the center and surround regions, and they were similar to the elevations evoked by flashes of longer duration. Secondly, ganglion cell responses to brief flashes exhibited the complete discharge pattern characteristic of the stimulated region, including typical off-responses, and with whole-field stimulation the response was derived from the activation of both mechanisms (center and surround) although the strength of each response (center and surround) had been reduced. As with longer flashes, center-dominance appeared at higher intensities. The difficulties in performing area-threshold analyses with brief flashes have already been mentioned and account for, I believe, the discrepancy in the findings of the two studies.

### Comparison of Latencies

The finding that center and surround responses occur at approximately equal latencies also contrasts with the conclusions of other investigators (12, 15). For example, Barlow, Hill, and Levick (15) showed, for unit responses in the rabbit retina, that the latency of the surround response was longer than the center response. The spot of light, however, was placed at a location in the receptive field where it evoked off-responses, and the latency of an on-response from one mechanism was compared with the off-response of the antagonist. In addition, since the stimulus activated both the center and surround mechanisms, the responses were actually based on the interaction of the two responses. Even when the stimulus was adjusted to produce center and surround responses of equal discharge frequency, it did not necessarily exclude an interaction between the center and surround mechanisms which would alter latencies. The latency of surround off-excitation, for example, would still be related to the strength and duration of the center off-inhibition. It is also probably safer to compare the latencies of like responses (e.g., on-responses vs on-responses) from the antagonistic regions. The identical objection can be raised with the analysis of latencies in the cat retina by Rodieck and Stone (12) who also concluded that surround responses occurred at longer latencies.

In the present study, when the stimulus was adjusted to evoke the optimal center or surround response and the latencies of on-responses compared, the difference between the center and surround regions was not significant. Nevertheless, it would still be predicted that a small spot of light placed within the surround would evoke a response at a longer latency than the same spot placed within the center (2, 12). There are at least four factors which would determine the latency: receptor density, distance from the ganglion cell, number of synapses, degree of spatial summation. The point made by the present finding is this. Despite the greater distance from the receptors to the ganglion cell within the surround, and possibly an additional synapse interposed in the pathway between receptor and ganglion cell (16, 17), there are sufficient number of receptors within the surround which summate to activate the ganglion cell at a relatively short latency.

## Relative Strengths of Center and Surround

Dominance of the response by the center mechanism was originally demonstrated by Kuffler (2) and has since been corroborated by other investigators working with spot-of-light stimulation (3, 12). In addition, in studies where the retina has been diffusely illuminated it has been assumed that the center mechanism contributes the dominant response pattern (18, 19). In the present study when the entire receptive field was stimulated at intensities greater than 1.0 log unit above threshold, the response, although weaker, usually resembled the response obtained by stimulating the center alone.

Only a few attempts have been made to quantify the relative strengths of the opposing receptive-field processes. By comparing the maximum amplitudes of responses to small spots (2.0'–4.0') flashed within the receptive field, Rodieck (20) estimated the ratio of center to surround strengths at 1:4. This value depends, of course, on the location of the points sampled within the receptive field and would vary with the radius of each point from the field's center. Since it does not reflect the relative strengths of the entire center and surround mechanisms, a higher value (0.8) was selected by Rodieck to represent the ratio of total surround strength to total center strength (20).

A second contribution in this area was recently made by Enroth-Cugell and Robson (13), since their method of stimulation provided a quantitative estimate of center and surround strengths. The retina was stimulated by grating patterns whose luminance varied sinusoidally with the distance between the bars. By altering the contrast and spatial frequency of the pattern, they were able to calculate the relative strengths of the entire center and surround areas. In 21 X-cells (cells that exhibited linear summation within the borders of the center or surround) the ratio varied between 0.73 and 0.98, and I calculated a mean of 0.9 (from the data presented in Table I of their report). Although the center was always stronger than the surround, the mean ratio is quite close to unity, and in 15 of the 21 cells it was actually  $\geq 0.90$ .

In the present study the thresholds of the center and surround with optimal stimuli were equal in 45 per cent of the sample, and in the remainder of the cells the mean difference in threshold was only 0.23 log unit. Wiesel (4) had also reported nearly equal thresholds for the center and surround in some fields and also described on-off responses to whole-field stimulation at threshold. For a threshold response to occur, it can be assumed that a minimum number of quanta must be absorbed by the receptor population forming the input from each receptive-field mechanism to the ganglion cell. Similarly, a minimum number of receptors would absorb these quanta. Since Enroth-Cugell and Robson (13) have demonstrated that summation is linear within each receptive-field mechanism, the local variations of receptor density within the center and surround would not be a significant factor determining the response. But this equivalence at threshold was lost at higher intensities when the center became dominant. For, in the present study, with whole-field stimulation, surround responses were

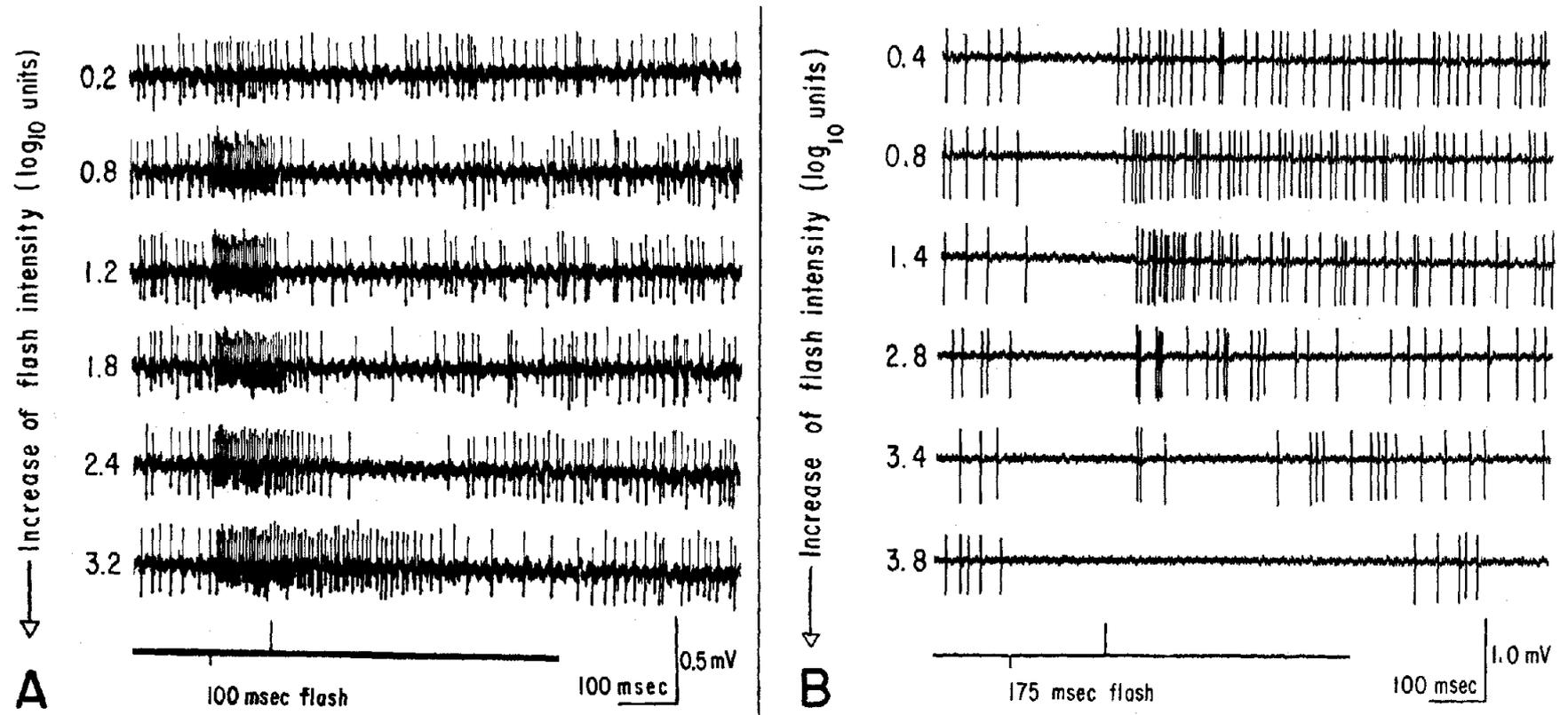
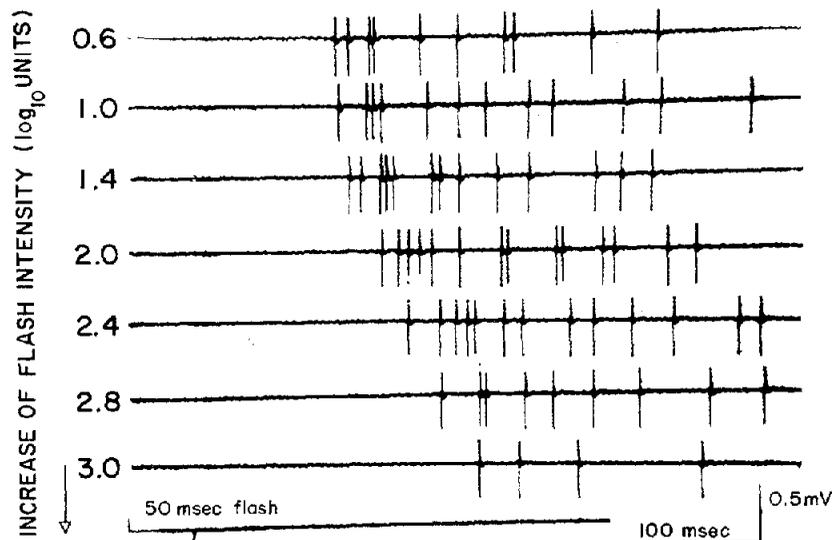
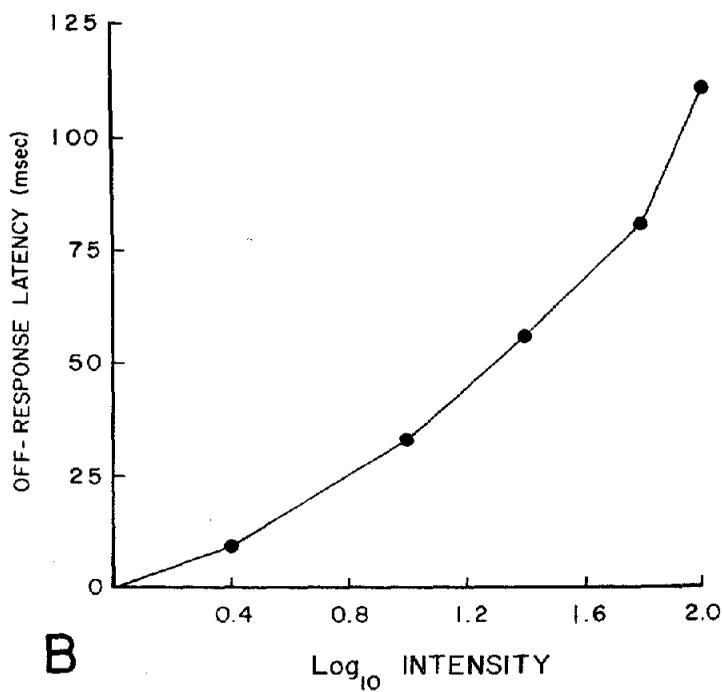


Figure 9

The center responses of two ganglions. A. Center response, on-excitation. Threshold intensity,  $1.8 \text{ lumens/m}^2$ ; adapting intensity,  $4.5 \text{ lumens/m}^2$ ; flash duration, 100 msec; optimal spot diameter, 0.33 mm. B. Center response, on-inhibition. Threshold intensity,  $0.45 \text{ lumens/m}^2$ ; adapting intensity,  $0.45 \text{ lumens/m}^2$ ; flash duration, 175 msec. Otherwise as in A.



**A**



**B**

Figure 10

Extension of the on-response, with optimal center stimulation, as a function of intensity. The responses to flashes of increasing intensity are presented in A, and the latencies to the first spike of the off-response are plotted vs  $\log_{10}$  intensity in B. The center response was on-inhibition. Threshold intensity, 2.8 lumens/m<sup>2</sup>; adapting intensity, 0.45 lumens/m<sup>2</sup>; flash duration, 50 msec; optimal center stimulus--0.33 mm in diameter. In this cell the off-response occurred at a long latency, even at optimal intensities, and the spontaneous activity was low because the retina had been depressed by a preceding period of hypotension.

## SURROUND RESPONSES

Stimulation of the surround with flashes that were optimal in area and location activated the center mechanism at high intensities ( $> 1.5$  log above the surround threshold), as has already been illustrated (Figure 5). In many fields, therefore, surround responses could not be studied with intense flashes because of these stray-light effects. However, when the surround response was strong relative to the center response, extension of the surround on-response was observed at high intensities of the flash. This effect is illustrated in Figure 11 in the responses of a cell to optimal stimulation of its surround, where the on-response was excitation. At moderate intensities (1.5), off-inhibition followed the on-excitation at a short latency. Extension of the on-excitation occurred at higher intensities (1.9) and increased in duration with further elevation of flash intensity (2.3 to 4.8). The intensity effect was identical, therefore, to that obtained with high-intensity stimulation of the center mechanism.

Stray-light effects still occurred at these intensities, and produced unusual discharge patterns. For example, at 2.7 log units above threshold (Figure 11) a period of inhibition (a center-type response) interrupted the on-excitation. The center response strengthened at higher intensities, and at 4.8 log units above threshold, on-inhibition and off-excitation (at a short latency) dominated the response. Nevertheless, the activation of the center mechanism, at high intensities, did not interfere with the extended portion of the surround's on-response which still appeared at a long latency following the "off" of the flash. The off-response of this cell was now derived from two sources, both excitatory; and the off-excitation of the center preceded and merged with the long-lasting extension of the on-excitation from the surround.

A complementary sequence is illustrated by Figure 12, where the on-response of the surround was inhibitory, and at high intensities the on-inhibition continued into the off-period (1.8 to 4.6). At 4.0 log units above threshold on-excitation from the center was activated by stray light, while at the maximum intensity (4.6) the center mechanism had strengthened relative to the surround and the on-response was followed by a long period of inhibition. In view of the responses of off-center cells under the same conditions (Figure 11) it may be assumed that the long-lasting portion of this inhibition was derived from the extended on-inhibition of the surround.

## OFF-RESPONSES

In addition to increasing in latency, off-responses showed other effects at high intensities. For example, in some cells, with flashes of long duration (500 msec) administered at relatively high levels of light adaptation (45 lumens/m<sup>2</sup>), the off-response weakened at the highest intensities of the flash. At first this effect seemed to be separate from the extension of the on-response. Further analysis of the responses to a range of flash durations and levels of adaptation demonstrated, however, that the weakening of the off-response was sequentially related to the other effects. Figure 13 presents an intensity series in which the off-response could be followed closely at high intensities.

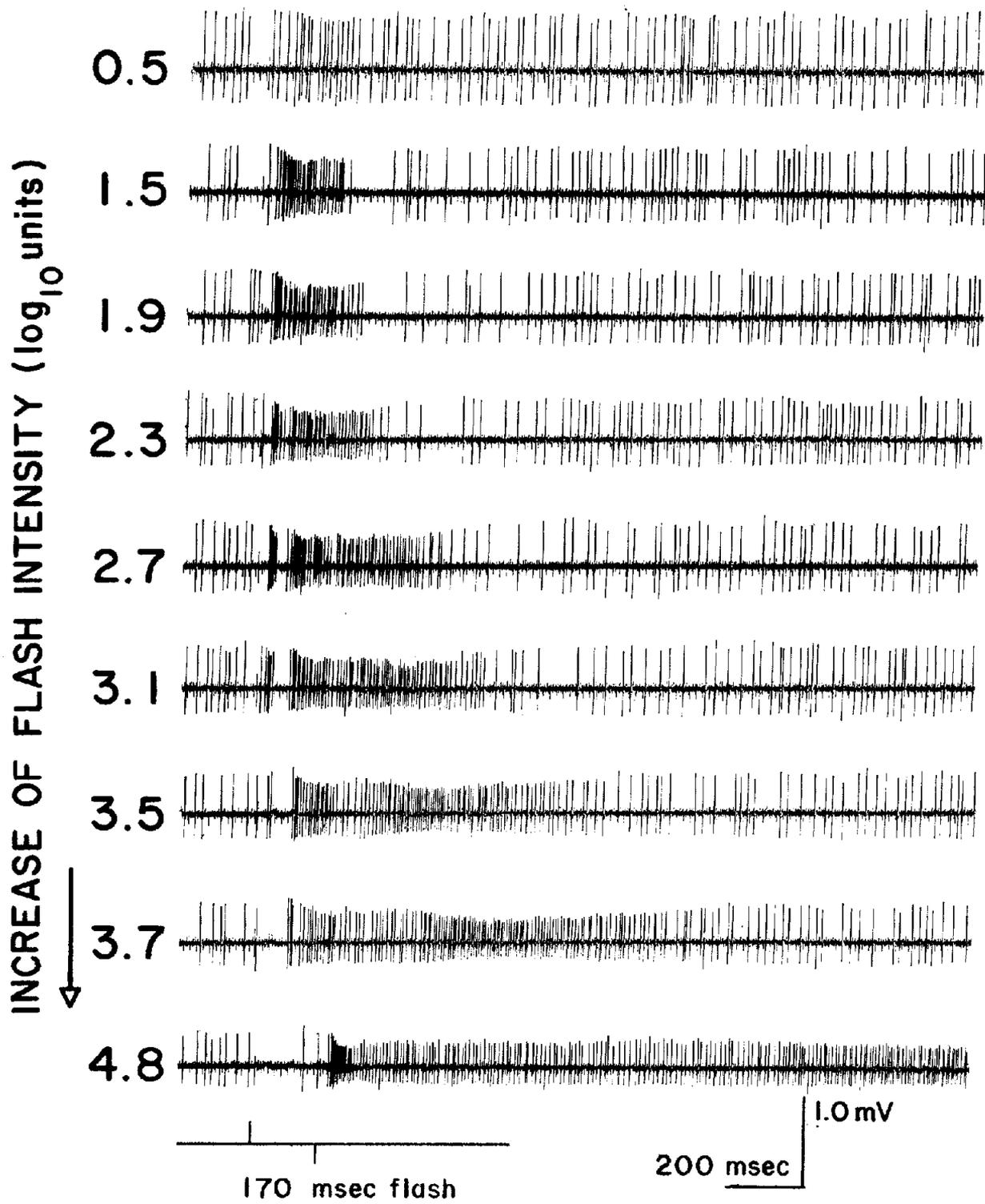


Figure 11

Extension of the on-response of the surround. The on-response of the surround was excitation. Optimal surround stimulus--inner diameter, 0.50 mm; outer diameter, 2.00 mm. Threshold intensity, 0.14 lumens/m<sup>2</sup>; adapting intensity, 0.45 lumens/m<sup>2</sup>; flash duration, 170 msec.

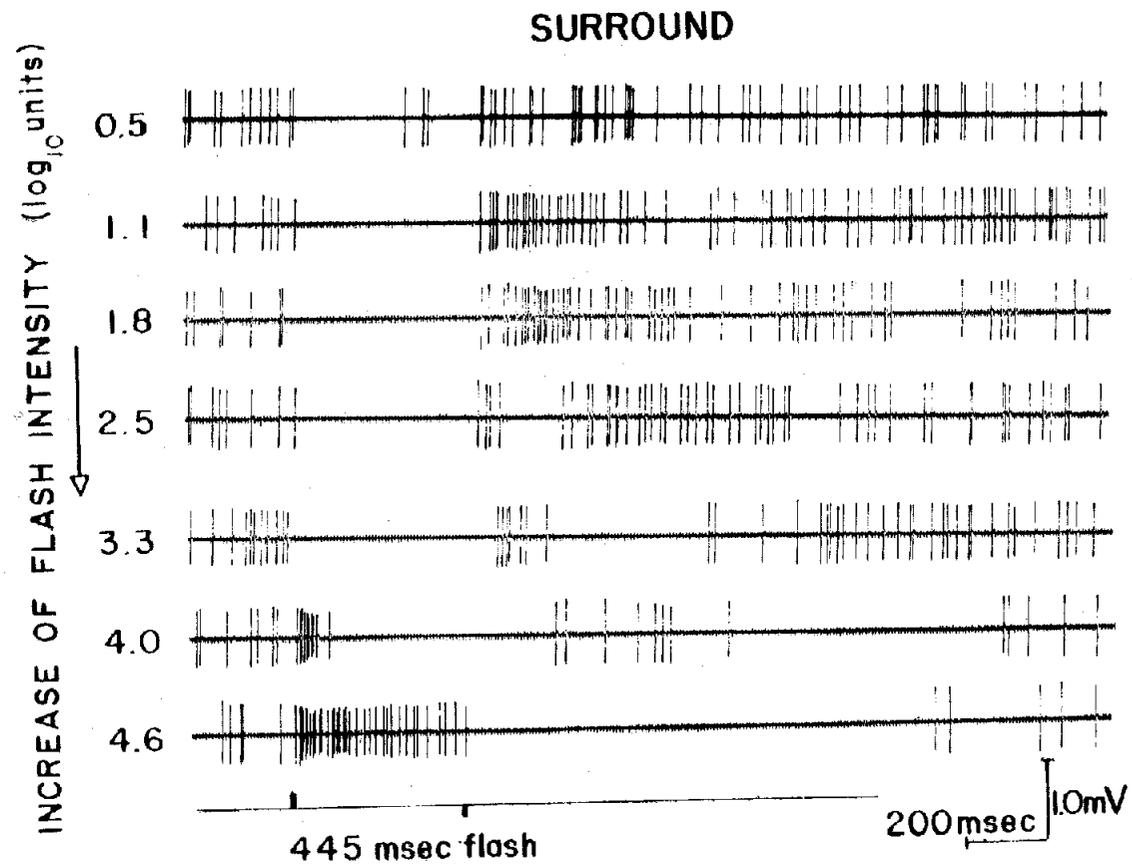


Figure 12

Extension of the on-response of the surround. The on-response of the surround was inhibition. Optimal surround stimulus--inner diameter, 0.33 mm, outer diameter, 2.00 mm. Threshold intensity, 0.18 lumens/m<sup>2</sup>; adapting intensity, 0.45 lumens/m<sup>2</sup>; flash duration, 445 msec.

(These are the center responses from the same cell whose surround responses were illustrated in Figure 11.) When on-inhibition extended into the off-period, the off-response, indicated by the point of highest discharge frequency, was observed at longer and longer latencies (2.4, 2.8). At still higher intensities (3.2 to 3.8) the off-excitation weakened, and at the maximum intensity (4.9) it could no longer be identified. Weakening of the off-response developed, therefore, as a late effect of extension.

A discontinuity in the off-response also often accompanied the increased latency. Thus, in Figure 13 a brief remnant of the off-discharge persisted at a shorter latency while the main body of the off-response was delayed (2.8 to 3.8). At the highest intensity (4.9) the remnant was also lost. This splitting of the off-response was more pronounced at longer durations of the flash. For example, in Figure 14 a distinct period of off-inhibition persisted at a relatively short latency in response to a 450 msec flash at the maximum intensity while at shorter durations of the flash (50 msec, 170 msec) this remnant was not present. It can be observed, however, at lower intensities (50 msec, 2.8; 170 msec, 2.8, 3.4).

### INTRACELLULAR RECORDING

Although many units were penetrated, stable intracellular recordings were extremely rare. Figures 15 and 16 were obtained from one cell that was studied for approximately 10 min. The largest spikes (ca. 20 mV) were observed immediately after penetration (Figure 15A). The stimulus for the responses of Figure 15A was a spot of light, 0.84 mm in diameter, that was located somewhere within the receptive field of this cell. The dominant slow-potential response to the flash (Figure 15A, top) was a depolarizing postsynaptic potential (PSP) of about 12 mV, upon which were superimposed one or more brief swings of the potential in a hyperpolarizing direction. The "off" of the flash led to a rapid hyperpolarization followed by a slow depolarization. The response of Figure 15A, bottom, differed since the position of the flash had been altered. In both cases depolarization (EPSP) was accompanied by discharge of the cell and hyperpolarization (IPSP) by inhibition. The steady-state PSP of the on-response, followed by a reversal of potential at the "off," resembled the intracellular recordings from cat ganglion cells published by others (3, 24).

Recordings obtained several minutes later (Figure 15B), after centering the spot at the microelectrode tip, exhibited a complete absence of impulses during the "on." At the beginning of the PSP, however, a burst of small spikes occurred, followed by a series of local potentials which did not lead to impulses. Since the amplitude of the spikes had diminished from A to B, it was assumed that this injured cell had depolarized further and that the EPSP's now produced a depolarization block. The recordings were still valuable, however, since the PSP's could be studied.

At this point, with the spot centered, flash duration was decreased to 170 msec and responses were recorded to a series of flashes of increasing intensity. Three of these responses are illustrated in Figure 16. At the lowest intensity, A, the depolarizing on-response abruptly terminated following the "off," and the spontaneous discharges

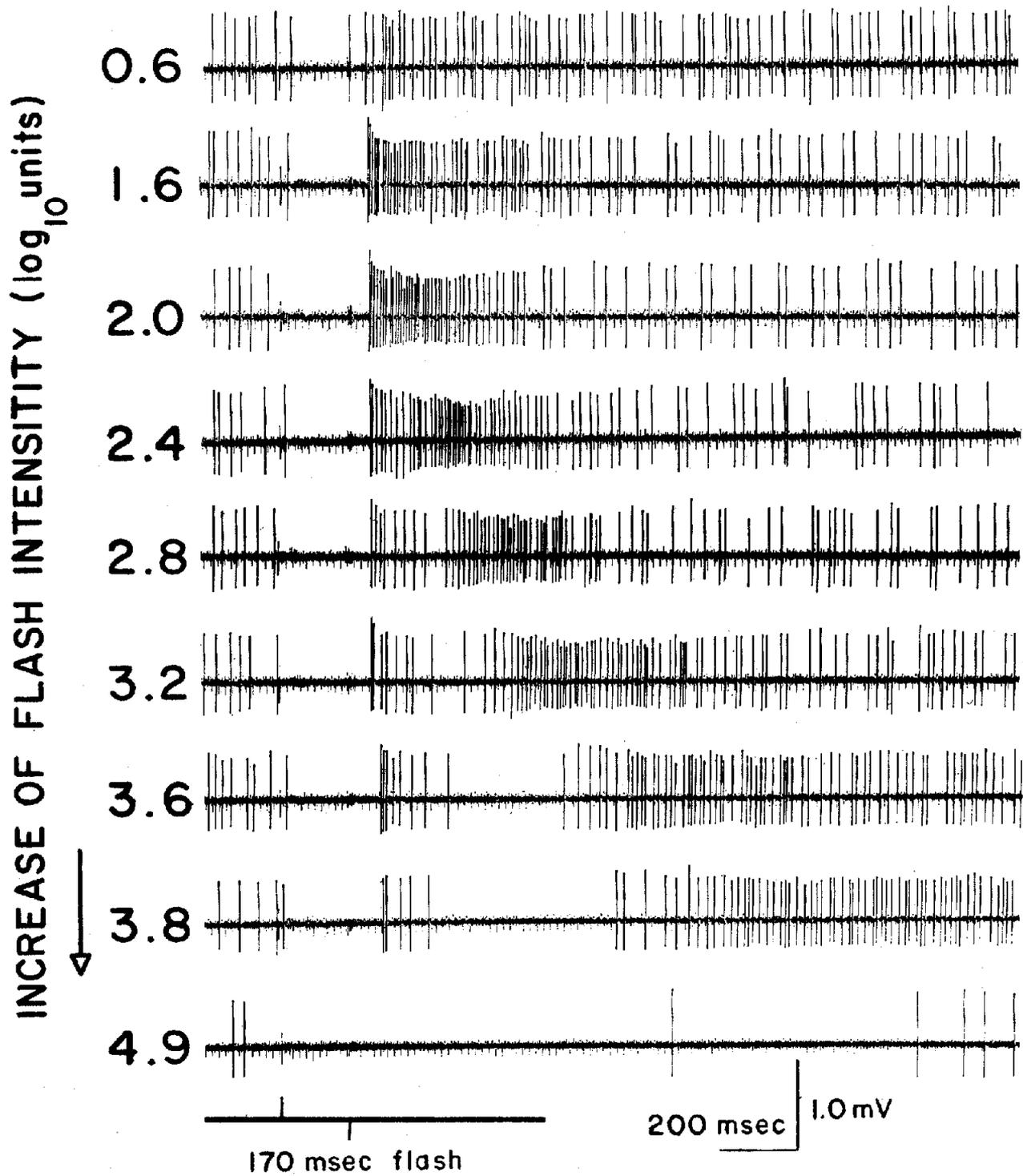


Figure 13

Extension of the on-response of the center as a function of intensity. The on-response of the center was inhibition. (From the same cell as Figure 11.) Optimal center stimulus, 0.33 mm in diameter; threshold intensity, 0.11 lumens/m<sup>2</sup>; adapting intensity, 0.45 lumens/m<sup>2</sup>; flash duration, 170 msec.

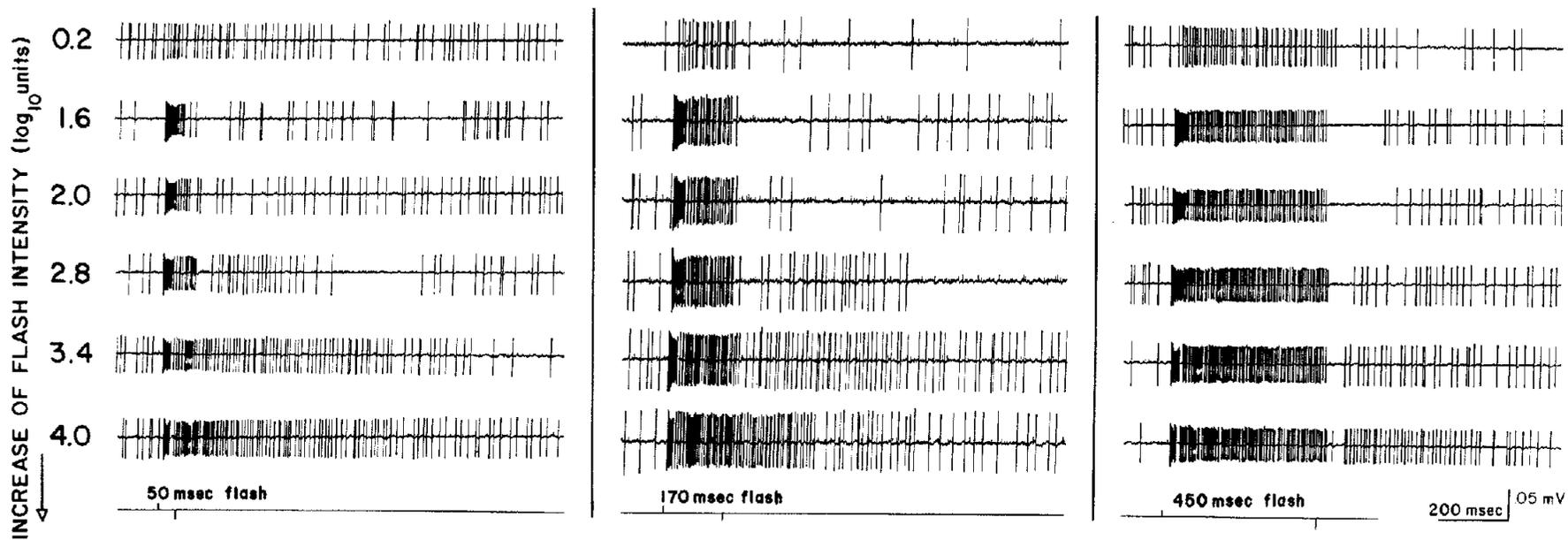


Figure 14

Extension of the on-response with optimal center stimulation at three flash durations (50 msec, 170 msec, 450 msec.) Optimal center stimulus, 0.33 mm in diameter; adapting intensity, 0.45 lumens/m<sup>2</sup>. Threshold intensities: 50 msec, 0.18 lumens/m<sup>2</sup>; 170 msec, 0.07 lumens/m<sup>2</sup>; 450 msec, 0.045 lumens/m<sup>2</sup>.

of the cell quickly returned. A 1.2 log unit increase of flash intensity, B, however, altered the course of the response following the "off" of the flash, since the repolarization that immediately followed the "off" decreased in amplitude and rate. Note that this abrupt repolarization was followed, now, by a slower repolarization which was accompanied by a gradual return of spikes. At the maximum intensity, C, these effects were more pronounced and the onset of the abrupt repolarization became delayed.

## PART II: DISCUSSION

### EXTENSION OF THE ON-RESPONSE

A number of similar high-intensity effects have been described previously in the literature. For example, Hartline (25) in the original description of single unit activity from the vertebrate eye, noted an unusual consequence of high-intensity flashes. The off-effect, defined as a burst of impulses at the "off" of the light, was reduced in strength or was completely absent at high intensities. This phenomenon was interpreted as originating in an inhibition of the off-response. Granit (26) confirmed this finding in single fiber recordings from the optic nerve of cat. He interpreted it as an example of post-excitatory inhibition which was usually observed after periods of on-excitation in some units. These two phenomenon, i.e., inhibition following on-excitation and the reduction of the off-effect at high intensities, can now be shown to originate from different mechanisms. Whereas the inhibition following on-excitation is an off-response, the high-intensity effect represents the loss of an off-response which results from a continuation of the on-response into the off-period. At high-flash intensities the ganglion cell can be inhibited or excited following the "off" in accordance with the sign of the on-response. The off-response is not inhibited, however; rather the data suggest that its loss results from a weakening of the off-response mechanism itself.

More recently, in the unopened eye of the cat Brown and Wiesel (3) described units whose response was purely inhibitory. These cells exhibited typical off-center fields and responded with long-lasting inhibition under certain conditions; i.e., when a small spot of light, focussed on the receptive-field center, was gradually elevated in intensity the off-discharge became delayed and then disappeared. These effects occurred at intensity levels similar to those observed in the present study. In an extreme case the inhibition lasted for 7.0 sec after the "off" of the flash. The description of pure inhibition and the example presented (Brown and Wiesel (3) Text--Figure 5, P. 551) appear to represent on-inhibition extended into the off-period in an off-center field.

Finally, two very recent reports in the literature present related findings. In the cyprinid fish Naka and Kishida (27) described a gradual increase in the latency of off-discharges brought about by increasing the intensity of retinal illumination. They noted that a 2.0 log unit increase in intensity did not increase the latency of the off-discharge, while above this level the increase in latency was a linear function of log

intensity. The report of Pickering and Varjú (28) described the effect of increasing the flash intensity on the responses from sustained edge-detectors in the frog retina. Again, the latency of the discharge increased, but as a power function of log intensity. Although the authors did not identify this response as an off-discharge, the optimal stimulus was a circular black disk ( $5^\circ$  visual angle) against a white background that was illuminated by a stroboscopic flash. This stimulus is ideally suited for stimulating off-center fields (29), evoking on-inhibition followed by off-excitation.

## GANGLION CELL ACTIVITY AND THE D.C. COMPONENT OF THE LERG

In an earlier report from this laboratory the response characteristics of the d.c. component of the local electroretinogram (LERG) were described (1). The d.c. component was characterized as a graded potential, having a small summation area, with its maximal amplitude in the inner nuclear layer. It was suggested that it might be the extracellular reflection of the generator potential which initiates ganglion cell activity. It is important, therefore, to examine the response characteristics of ganglion cells to determine if they are compatible with those described for the d.c. component.

### High-Intensity Effects

The most prominent finding relating the d.c. component to the response of ganglion cells is the high-intensity effect. High intensities of retinal illumination evoked parallel changes in the responses of both the d.c. component and ganglion cells. Extension of the on-response (ganglion cell) closely resembled the increase in duration of the d.c. component. Although the ganglion cell effect occurred at a lower absolute intensity (compatible with its lower threshold), in both the change in response duration was observed only after an initial increase in intensity of about 2.0 log units. They were both linear functions of log intensity, and both occurred across a wide range of flash durations where they were quite similar in form at each duration (e.g., brief flashes evoked large increases in duration relative to the duration of the stimulus). Extension of the on-response appeared to be characteristic of the input to the cell, regardless of its source or sign, for it was equally distinct with inhibition and excitation and occurred with stimulation of either the center or surround. Within the highly sensitive center area it was produced by stimuli of very little area, and, therefore, spatial summation from a large area was not required.

The off-response of the ganglion cell and the decay of the d.c. component were also similarly affected at high intensities, since both were delayed and both diminished in amplitude. At high intensities the rate of decay of the d.c. component gradually decreased while at the highest levels of illumination, the abrupt decay was lost, and only a very gradual decay towards the baseline remained. This effect is directly analogous to the gradual diminution in the amplitude of the ganglion cell's off-response which finally led to the complete loss of the off-response at the highest intensities. The

strength of the ganglion cell's off-response, therefore, seems directly related to the rate of decay of the d.c. component. Presumably, the time constant of decay must reach a minimum value before an off-response can be observed.

The persistence of a remnant of the off-response (ganglion cell) at high-flash intensities, especially with flashes of longer duration (500 msec), resembled the early off-response of the d.c. component which was also more pronounced at long durations of the flash. At high intensities, however, since the remnant off-response of the ganglion cell's off-response weakened, while the early off-response of the d.c. component strengthened and shortened in latency, these effects may not be related. Possibly at higher flash intensities than were available, suppression of this early decay of the d.c. component might also have been observed.

The data obtained from the intracellular recording showed clearly that the high-intensity effect was already present in the input to the cell since the post synaptic potential reflects this input. Extension of the on-response does not arise, therefore, from an after-effect of ganglion cell activity, e.g., as an after-effect following strong depolarization or hyperpolarization, but is the response of the cell to an event which originates at a more peripheral level of the retina. The behavior of the PSP is closely related to the behavior of the d.c. component, since the PSP increases in duration and undergoes a decrease in its rate of repolarization at high-flash intensities. The action-spike responses of the ganglion cell directly reflect these changes of the PSP; an increase in the duration of the PSP produces an increase in duration of the on-response. With regard to the off-response, the decrease in decay rate weakens the off-response, while the persistence of a short-latency, low-amplitude period of repolarization may evoke the off-response remnant.

### The Effect of Flash Duration

Alterations in flash duration generally had similar effects on the d.c. component and ganglion cell activity. The response of the d.c. component to short-duration flashes had been studied at relatively high levels of light adaptation and with flashes of small diameter in order to isolate the response. The complete response, consisting of an onset, plateau, and decay, was observed in response to brief (10 msec) flashes. Similarly, ganglion cell responses to flashes of this duration were also complete. In particular, distinct off-responses were usually observed.

When the duration of the flash was increased by 10 msec increments, neither the on-response of the ganglion cell nor the plateau of the d.c. component increased in duration by the full increment of the flash until flash duration reached a minimum of about 50 msec. The late receptor potential also behaved in a similar manner; it did not increase by the full increment until the flash reached a minimum duration (1). Although the actual duration of the response was a function of intensity, this characteristic appeared through a wide range of intensities (excluding very high and very low intensities). It suggested that the briefest flashes evoked a fixed duration response from the receptors which was transmitted to the ganglion cell.

At longer durations of the flash ( $> 100$  msec) the strength and latency of the ganglion cell's off-response were enhanced. However, a similar enhancement of the decay of the d.c. component did not occur. Its amplitude and rate of decay did not significantly increase with increases in duration of the flash. If the d.c. component is closely related to the generation of ganglion cell responses, then this facilitation would originate central to the generator of the d.c. component. Certainly it could originate in the ganglion cell itself but here it would not be from the buildup of a rebound from the preceding on-response since an off-response may actually be preceded by a strong response of the same sign; e.g., on-excitation evoked by stray light merged with the off-excitation of the surround mechanism.

It would appear, then, that the responses of ganglion cells, particularly with regard to the effects of flash duration and intensity, exhibit many of the same characteristics as the d.c. component of the local electroretinogram. However, since the late receptor potential also exhibits many of these characteristics, the relationship between d.c. component and ganglion cell may only be through this third source. There is no more conclusive evidence, as yet, that the d.c. component is directly related to the activation of ganglion cells, i.e., as a generator potential.

#### THE ON-RESPONSE AND AFTERIMAGES

If it be assumed that the discharge of ganglion cells initiates events at higher levels of the central nervous system which ultimately form the primary visual image, then the extension of the on-response should be represented there as a persistence of the image in time. Again, if there is a direct correspondence between the retinal output and the image with simple stimuli such as flashes, then it can be predicated that, at high intensities, the flash would appear longer, and it would be difficult to estimate exactly when the flash went "off."

Recent psychophysical evidence suggests that these retinal effects at high intensities are, in fact, related to perceptual events. Although the literature on afterimages is extensive, it is difficult to find data regarding events which occur within the first seconds after the "off" [for a recent discussion and review of afterimages see J. L. Brown (30).] In a study of the positive afterimage, however, following brief high-intensity flashes (0.5 to 5.0 msec;  $3 \times 10^7$  to  $10^{10}$  td. sec) observers reported that a dark period did not occur between the termination of the primary sensation from the flash and the onset of the positive afterimage (31). In fact, the positive afterimage began without a detectable latency, and the total appearance was that of a longer flash (31, 32); since the positive afterimage appeared to be a continuation of the flash, it was difficult to estimate the "off" of the flash (32).\*

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\*A lingering of the primary image with high-intensity flashes has at times been distinguished from the positive afterimage and referred to as persistence of vision (30, 33). It has been observed to last for a second or less, while rapidly decreasing in intensity.

(32). Perhaps this can be related to the remnant of the off-response which persists at high intensities and tends to be more prominent at longer flash durations. These apparent relations with extension of the on-response of ganglion cells would seem to be limited to the first phase of the positive afterimage, since afterimages persist for many minutes while extension has been measured only in seconds. It can be predicted from this association that neuronal activity at higher levels of the visual system (lateral geniculate nucleus, visual cortex) would exhibit related effects at high intensities.

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