TRANSIENT AND STEADY STATE RESPONSES OF CAT OPTIC TRACT FIBERS TO CHANGES IN LUMINANCE AND SIZE OF STIMULI

Thesis for the Degree of Ph. D.

MICHIGAN STATE UNIVERSITY
RAY WYATT WINTERS

1969

This is to certify that the

thesis entitled

TRANSIENT AND STEADY STATE RESPONSES OF CAT OPTIC TRACT FIBERS TO CHANGES IN LUMINANCE AND SIZE OF STIMULI

presented by

Ray Wyatt Winters

has been accepted towards fulfillment of the requirements for

Ph.D. degree in Psychology

Major professor

Date August 15, 1969

O-169

ABSTRACT

TRANSIENT AND STEADY STATE RESPONSES OF CAT OPTIC TRACT FIBERS TO CHANGES IN LUMINANCE AND SIZE OF STIMULI

By

Ray Wyatt Winters

Single unit recordings were made from cat optic tract fibers while varying the luminance and size of spots placed in the center of a cell's receptive field. Both transient and steady state stimulus-response curves could be divided into two segments: a monotonic increasing portion for low contrast levels (less than 2.2 log units above threshold) and a non-monotonic decreasing segment for high contrast levels (above 2.2 threshold units), with a greater amount of high contrast decline for off-center cells. The shape of the stimulus-response functions were not found to vary significantly for different spot sizes.

Three conclusions were made: (1) that cat retinal ganglion cells give a more precise representation of intensity changes in the low contract range; (2) that the intensity code is non-linear for this range; (3) that more information about intensity changes is signalled

during the transient component, than during the steady state component of the response.

The results were interpreted in terms of receptive field models presented by Rodieck and Stone (1965) and Rodieck (1967).

Approved By:_____

Date:_____

Thesis Committee:

Dr. S. Howard Bartley, Chairman
Dr. Glenn I. Hatton
Dr. John I. Johnson
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Ray Wyatt Winters

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Psychology

1969

ACKNOWLEDGMENTS

As is so often the case, it is not practical to name all of the people who have assisted me in this research project. Nevertheless, my gratitude is extended to all of them.

I am most assuredly indebted to the chairman of my guidance committee, Dr. S. Howard Bartley. I will always remember him as a friend as well as a teacher. I am also grateful to Dr. Richard J. Ball, Dr. Glenn I. Hatton, Dr. John I. Johnson and Dr. Robert L. Raisler for their assistance and guidance during my graduate training.

I also wish to thank: Andy Harton for his assistance in histology; John Haight for his advise on electronic matters; Stan Cohen for help with the statistics; and Rick Bectal, Terry Hickey, Larry Hutton and Mike Kelley for their assistance in every phase of the research.

I cannot overemphasize the importance of Jim Walters' timely assistance and encouragement. I cannot imagine this research being completed without his help.

The extreme patience and support shown by my wife are immeasurable. I thank her for being so understanding.

This research was supported by predoctoral fellowship 5-F1-MH-38, 110-02 (PS), NIH Grants NB05982 and

GM10890 and NASA contract NSG-475. It was conducted in the Laboratory of Comparative Neurology, Departments of Biophysics, Psychology, and Zoology, Michigan State University.

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INTRODUCTION

The stimulus dimensions of wavelength and intensity have, for the most part, been overlooked by investigators concerned with cat retinal ganglion cell activity (Bishop, 1967). Extensive examinations of the effects of these stimulus dimensions can be found only in several studies conducted by Granit (1944, 1947, 1955).

From Granit's 1947 and 1955 studies it can be concluded that cats have very few retinal ganglion cells which relay information that could be used as a basis for spectral discrimination. Opponent process cells (i.e. color coded cells), which have been found to be predominant in mammals which show spectral vision (DeValois 1965, Gouras 1968, Michael 1968, Wiesel and Hubel 1966), were rarely encountered with cats. Behavioral research (Mello and Peterson 1964, Meyer and Anderson 1965, Sechzer and Brown 1964) also suggests that cats are relatively deficient in spectral vision.

In 1944 Granit studied the effect of variation of intensity of photic stimulation upon the activity of single retinal ganglion cells. To date, this study has been the most extensive investigation of intensity coding in the cat's retina. The stimulus that Granit used

was a diffuse, one second photic pulse whose intensity was manipulated over a 6 log unit range. The pulse was shone directly into the cat's eye. For some cells, firing rates were measured during a one second period of time after stimulus onset. For others, firing rates were observed at the cessation of stimulation. His results showed irregular relations between intensity and firing rate with very few cells showing the same stimulus-response[1] functions. Relationships were only monotonic over limited ranges. In light of the cat's excellent ability to discriminate intensities (Mead, 1942), Granit's results were somewhat puzzling. At best, it can be said that he did not find the code for intensity.

The present study was designed to ask the same basic question that was asked in Granit's 1944 investigation: how do single retinal ganglion cells signal relative intensity changes? The approach, however, differs from Granit's in two major ways: (1) Granit varied the intensity of large, diffuse, luminous spots. In the present study intensity was manipulated for small focal stimuli placed in the center of a unit's receptive field. (2) Granit measured response magnitude by counting the number of spikes that occurred during a one second period

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[1]"Response" is used here to refer to spike activity of single retinal ganglion cells. Response magnitude refers to the number of spikes per unit of time.

of time. In the present investigation transient and steady state components of a response were analyzed separately. The rationale for the two modifications just mentioned is given below.

Although there are several exceptions (Rodieck 1967b, Spinelli 1966, Stone and Fabian 1966), most research (Bishop 1967) has shown that cat retinal ganglion cells have receptive fields in which center and surround regions are mutually antagonistic. Two types of cells are usually found: on-center, off-surround cells and off-center, on-surround cells. For an on-center cell, presenting a luminous spot in the center of the receptive field causes an increase in firing at the stimulus onset. A luminous pulse presented in the surround of the receptive field causes an increase in firing at the pulse's termination. The response for center and surround are reversed for off-center cells. Since the central regions are more sensitive than the surround regions (Kuffler 1953, Rodieck and Stone 1965), the more effective stimuli are ones which primarily activate the center of the receptive field, i.e., are not large enough to invade the surround. Using diffuse spots as stimuli as Granit did, would maximize spatial antagonism and thus lead to minimal activation of the cell. His use of other than optimal stimuli may have been the reason that he found irregular stimulus-reponse relationships. In any case, it seems more reasonable to use

stimuli which maximally trigger the cell under scrutiny. Therefore, intensity coding mechanisms were investigated in the present study with small luminous spots placed in the center of a unit's receptive field.

Rodieck and Stone (1965) have shown reliable time course changes in the response of single ganglion cells to luminous pulses. For an on-center cell, for example, there is an initial burst of firing followed by an exponential decay to a firing rate of about 1/5 the magnitude of the initial phase of the response. For a one second luminous pulse, the firing rate remains at this level until the illumination terminates. The initial phase, which lasts about 75 msec. is called the transient component of the response. Firing rates can reach as high as 700 spikes/second during this phase. For a one second luminous pulse Rodieck and Stone defined the activity during the last 300 msec. of the pulse as the steady state component. Firing rates for this component reach as high as 175 spikes/second. Off-center cells show a similar sequence at stimulus termination. The transient firing rate, however, returns to the maintained (spontaneous) level rather than to an intermediary magnitude. According to Rodieck and Stone the transient phase, for an on-center cell, for the most part, represents the effects of excitatory inputs to the cell while the steady state component reflects the sum of both excitatory and

inhibitory inputs. For an off-center cell the transient component is thought to be the result of the release of inhibitory influences. Granit measured response magnitude by summing spikes over a one second period. Differences in the signals of intensity changes coming during the transient and steady state components could have been concealed by this measure. Thus, in the present study transient and steady state components of the response were analyzed separately.

The value of the approach advocated here has been demonstrated by a recent study by Stone and Fabian (1968). In varying the intensity of a small luminous pulse placed in the center of a unit's receptive field, they found a monotonic relationship between stimulus magnitude and the maximum firing rate (of the transient component). The shapes of the stimulus-response functions under these conditions--in contrast to those found by Granit--were the same for all retinal ganglion cells studied. Their primary concern was not intensity coding mechanisms so they only examined the effects of low contrast stimuli. They did not examine changes in the response of the steady state component nor did they observe the effects of more than one size of spot.

The present investigation can be considered as an expansion of the Stone and Fabian study. It was intended as a step toward understanding intensity coding

mechanisms in the cat's retina. The mechanisms were studied under the following conditions: (1) small luminous pulses (from .1° to 7.0°) were placed in the center of a unit's receptive field, (2) pulses were 920 msec. in duration, (3) ambient background levels were 0 or 1 log candle/m^2, (4) photic intensities ranged up to 4.2 log units above threshold.

METHOD

Subjects and Apparatus

Single unit recordings were made from 81 (44 on-center cells and 37 off-center cells) optic tract fibers of normal, adult cats. The cats faced a diffusely lit (either 0 or 1 log candle/m^2) 1-1/2 meter translucent tangent screen. The photic source, a modified 750 watt slide projector was placed behind the screen. The size of the luminous spots flashed on the screen was controlled by placing metal slides in the projector. A metal neutral density filter holder and a variable speed shutter were attached to the movable lens of the projector.

Recording System

Glass insulated tungsten microelectrodes were used in a conventional capacitance coupled recording system. After being amplified and filtered for low frequencies, spike activity was passed through a Schmitt trigger circuit. The Schmitt trigger output was fed to an audio monitor and to one channel of a tape recorder. The second channel of the tape recorder was used to record pulses that were synchronized with the stimulus.

Procedure

All surgery including cannulation of the femoral vein, a bilateral cervical sympathectomy (to minimize eye movements, Rodieck et al. 1967), tracheotomy, crainotomy, and the mounting of the cat's head in a head holder was performed under Pento Short (a short acting bartituate given intravenously).

Upon completion of surgery the animals were electrically decerebrated by a technique similar to the one described by Martin and Branch (1958). In order to immobilize the eyes an intravenous injection of 80 mg of Flaxedil was given. A mixture of this drug (28 mg/hour) and physiological saline (6 cc/hour) was continously infused through the femoral vein for the duration of the experiment. Respiration was maintained by a Harvard Apparatus respirator pump (stroke volume 45 cc; rate, 20/minute). Body temperature was held at 38° C by a heating blanket connected in a 12 volt D.C. circuit.

Corneal contact lens were fitted to prevent corneal clouding. A ten per cent solution of neosynephrine was used to keep the pupils dilated. Retinoscopy was performed in the usual manner with spherical and cylindrical lens appropriately placed in front of the eyes to correct refractive errors.

The methods used for locating the optic tract were the same as those outlined by Bishop et al., 1962a.

Once a fiber was isolated its receptive field was mapped from the rear of the tangent screen with .1°, luminous spots.

Threshold Studies.--Thresholds for various sized spots--placed in the most sensitive portion of the receptive field--were determined by varying their intensity in .1 log unit steps while listening to changes in activity over the audio monitor, i.e. the signal which had been filtered and passed through the Schmitt trigger circuit. For eight of the 21 cells studied, thresholds were also determined by analyzing changes in maintained (spontaneous) firing rates with a computer of average transients (C.A.T.). The threshold values from the two techniques were never more than .1 log unit apart.

Suprathreshold Studies.--The luminance of various spots, ranging from .1° to 7°, was varied in .3 log unit increments over a 4.2 log unit range. Because most diffusing surfaces are directional, luminances have been expressed in threshold units i.e. log units above threshold intensity or in terms of neutral density filter values (where smaller values represent greater luminance levels.) The duration of stimulus pulses was 920 msec.; their rise time was 5 msec. Each stimulus was repeated 15 times at a rate of .2 cycles/second and was presented in the most sensitive portion of the receptive field. Figure 1 shows how response magnitudes were measured.

Figure 1.--Schematic delineating how response magnitudes were measured for on-center and off-center cells. Two response measures were used for on-center cells; (1) the average firing rate (for 15 stimulus cycles) during the first 75 msec. of the response, i.e., the transient component; (2) the average firing rate during the last 300 msec. of the response--the steady state component. Because the steady state component for off-center cells was the same as the maintained (spontaneous) firing level, only the transient phase of the response was measured for these cells.

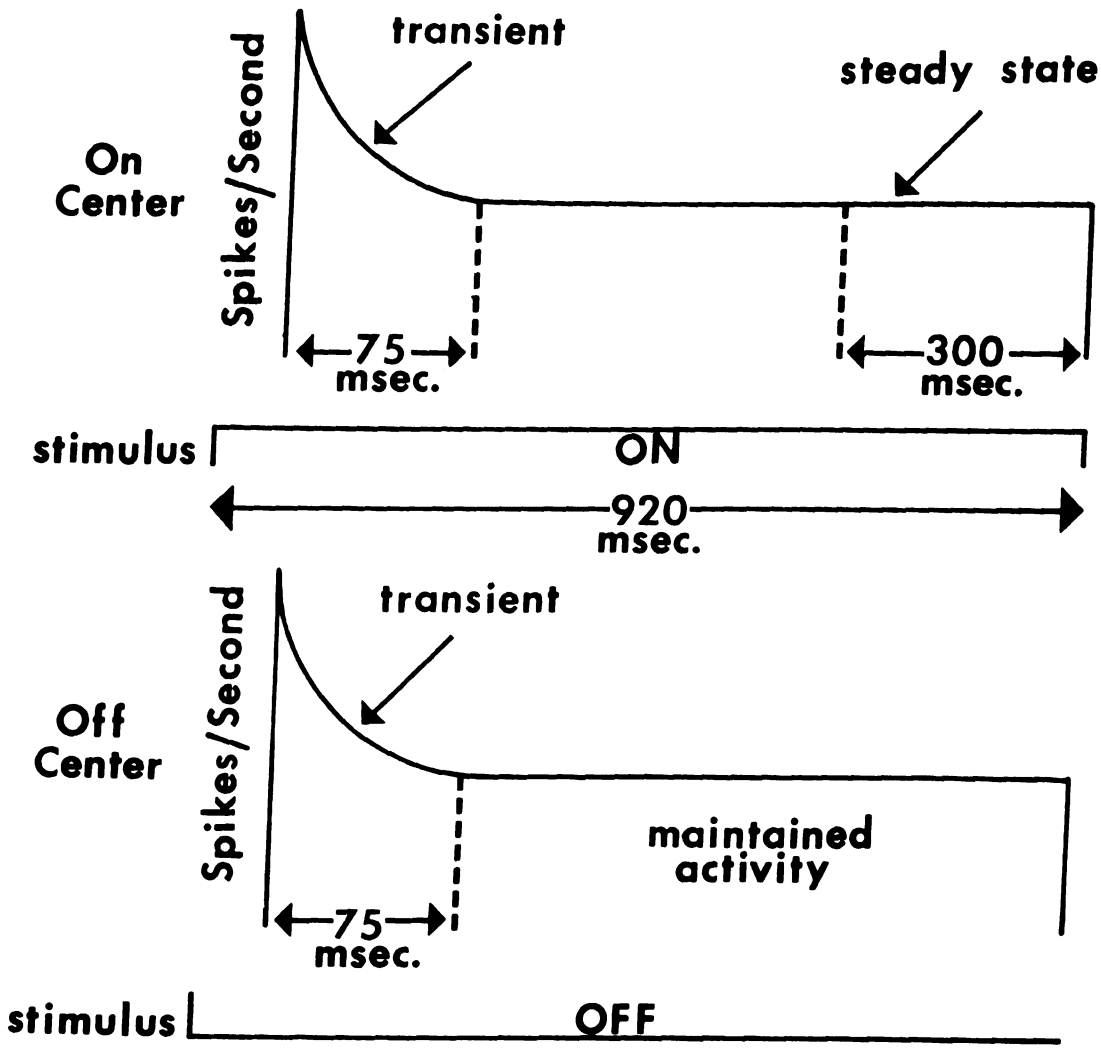
transient
steady state
On
Center
Spikes/Second
75
msec.
300
msec.
stimulus
ON
920
msec.
transient
Off
Center
Spikes/Second
maintained
activity
75
msec.
stimulus
OFF

Figure 1

Upon completion of recording from a unit, its receptive field location, with respect to the area centralis, was determined by the reversible opthalmoscopic technique (Bishop et al., 1962b). After completing work in a puncture a microlesion was placed at the recording site. Recording locations were histologically confirmed.

RESULTS

Confirming the reports of other investigators (Hubel 1960, Kuffler 1953, Wiesel 1960, Rodieck and Stone 1965) the optic tract fibers that were studied showed concentrically arranged receptive fields where center and surround regions were mutually antagonistic. The less common types of receptive fields reported by Rodieck 1967b, Spinelli 1966, and Stone and Fabian 1966, were not encountered.

The central regions of the receptive fields ranged from .6° to 7° in diameter (at the widest margins) with smaller receptive fields, in general, being found nearer the area centralis (Figure 2). Mapping experiments demonstrated that the central portion of the fields were more sensitive than surround regions (Kuffler 1953, Rodieck and Stone 1965). Thus, as a rule, units could be categorized by their response to ambient illumination: on-center, off-surround cells gave an on response and off-center, on-surround cells gave an off response.

Area-Threshold Studies

Area-threshold curves were determined for 12 on-center cells and 9 off-center cells. Most of the functions

Figure 2.--Approximate retinal locations of receptive fields of units recorded from the left optic tract, as inferred from the reversible ophthalmoscopic tachnique. All points in the 1st and 4th quadrants represent receptive fields from the nasal hemiretina of the right eye. Points at greater distances to the right of the origin are more nasal to the area centralis of the right eye. All points in the second and third quadrants represent fields in the temporal hemiretina of the left eye. Points at greater distances to the left of the origin are more temporal to the area centralis of the left eye. The origin of the graph represents the area centralis for both the left and right eyes. The two dots which lie on the vertical axis represent right eye receptive fields. Dots symbolize on-center cells; triangles symbolize off-center cells, with sizes proportional to receptive field center size. Three nasal units from the right eye are not plotted. Maps were not made for five units.

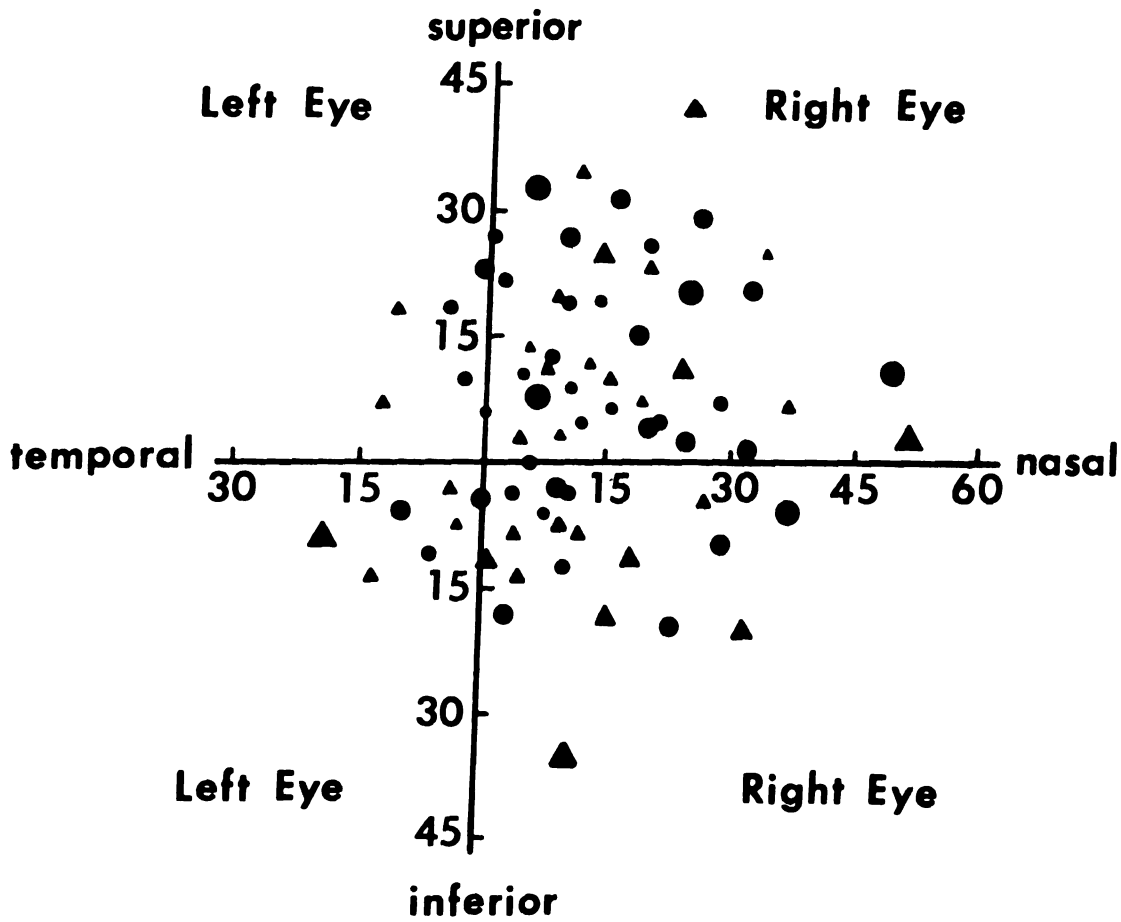
superior
Left Eye
Right Eye
45
30
15
temporal
30
15
15
30
45
60
nasal
15
30
Left Eye
Right Eye
45
inferior

Figure 2

were similar in shape to the one shown by the cell in Figure 3. Starting with the smallest spot, increasing spot size resulted in a drop in threshold until the edge of the central region--as determined by the mapping technique--was reached. Beyond this point the curves either became horizontal or a small increase--no greater than 1/3 of a log unit--in threshold occurred. The mean value of the slope of a least squares straight line fitted to the decreasing portion of the curve was determined to be -1.48 (S.D. = .54) for the 12 on-center cells and -1.43 (S.D. = .41) for the 9 off-center cells. A "t" test comparing these two means showed them not significantly different ($t = .12$, $df = 19$, $p < .20$). Slopes in the range of -1.45 fall between those predicted by Ricco's and Piper's laws. (Figure 3)

Suprathreshold Studies: High vs Low Contrast Stimuli

On-Center Cells.--As Figure 4 shows, intensity variation had similar effects upon the shape of the transient and steady state component stimulus-response curves. The functions shown in the figure can be divided into two segments: an increasing portion for low contrast levels (up to about 2.2 log units above threshold) and a decreasing segment for high contrast levels (beyond 2.2 log units above threshold). The low contrast portion of the curve was generally monotonic for both components

Figure 3.--Area-threshold curve for typical on-center cell plotted on log-log coordinates. The slope for a least squares straight line is -1.45. The slope predicted by Ricco's law (area x intensity = constant) is -2. The slope for Piper's law ($\sqrt{\text{area}}$ x intensity = constant) is -1. Background intensity = 0 log candles/m^2.

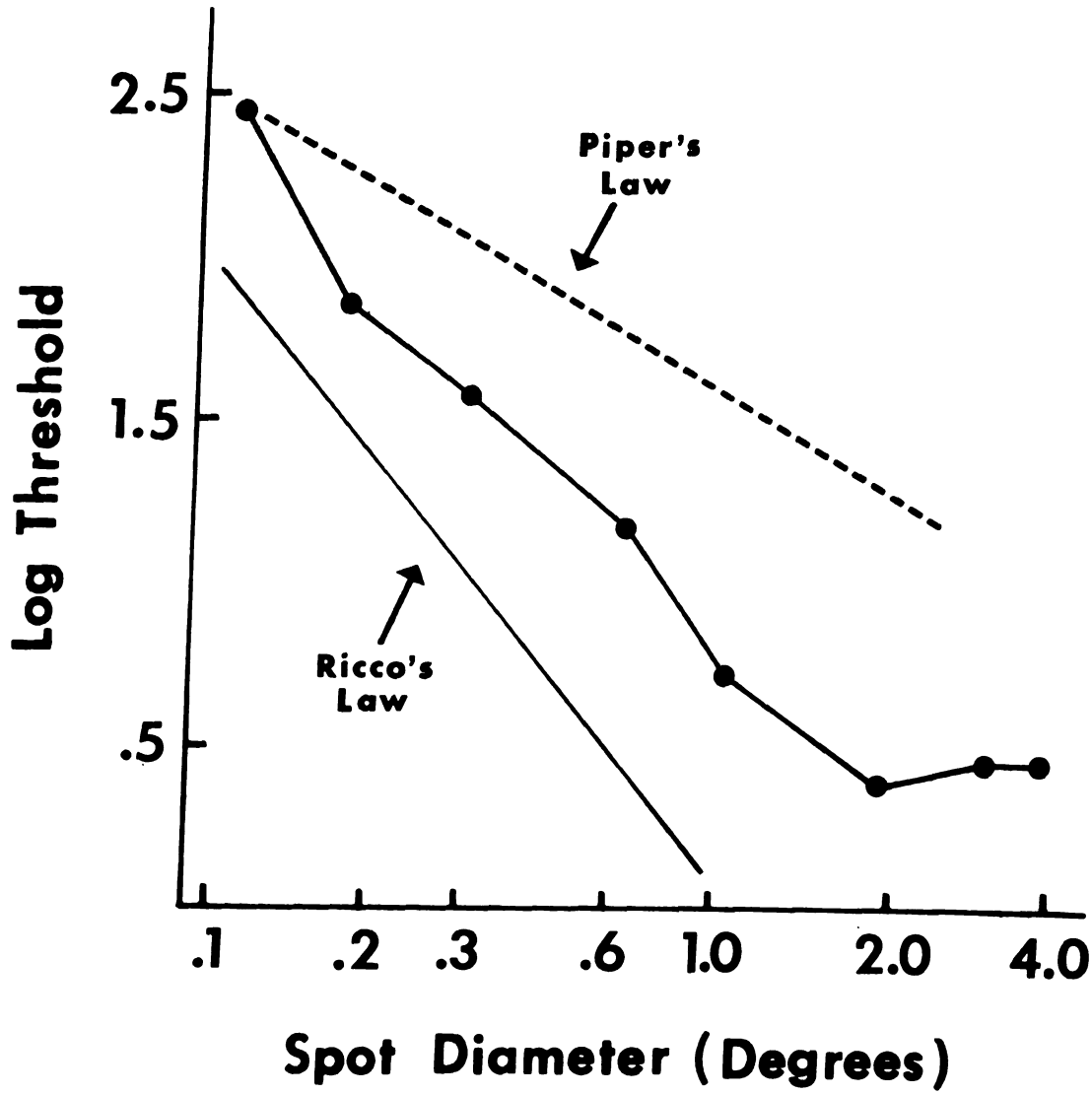
2.5
1.5
.5
Log Threshold
Piper's Law
Ricco's Law
.1
.2
.3
.6
1.0
2.0
4.0
Spot Diameter (Degrees)

Figure 3

Figure 4.--Transient and steady state stimulus-response functions for an on-center cell. The data are plotted on semilog coordinates in the lower graph; on linear coordinates for upper left graph (for low contrast levels only); on log-log coordinates for upper right graph. Values on the abscissa are expressed in threshold units. Bars around the points in the lower graph are 99 per cent confidence intervals. Spot size = 0.8°, in right eye receptive field with 1.2° center, located at a position 16° nasal and 7° superior to the area centralis. Background intensity = 0 log candles/m^2.

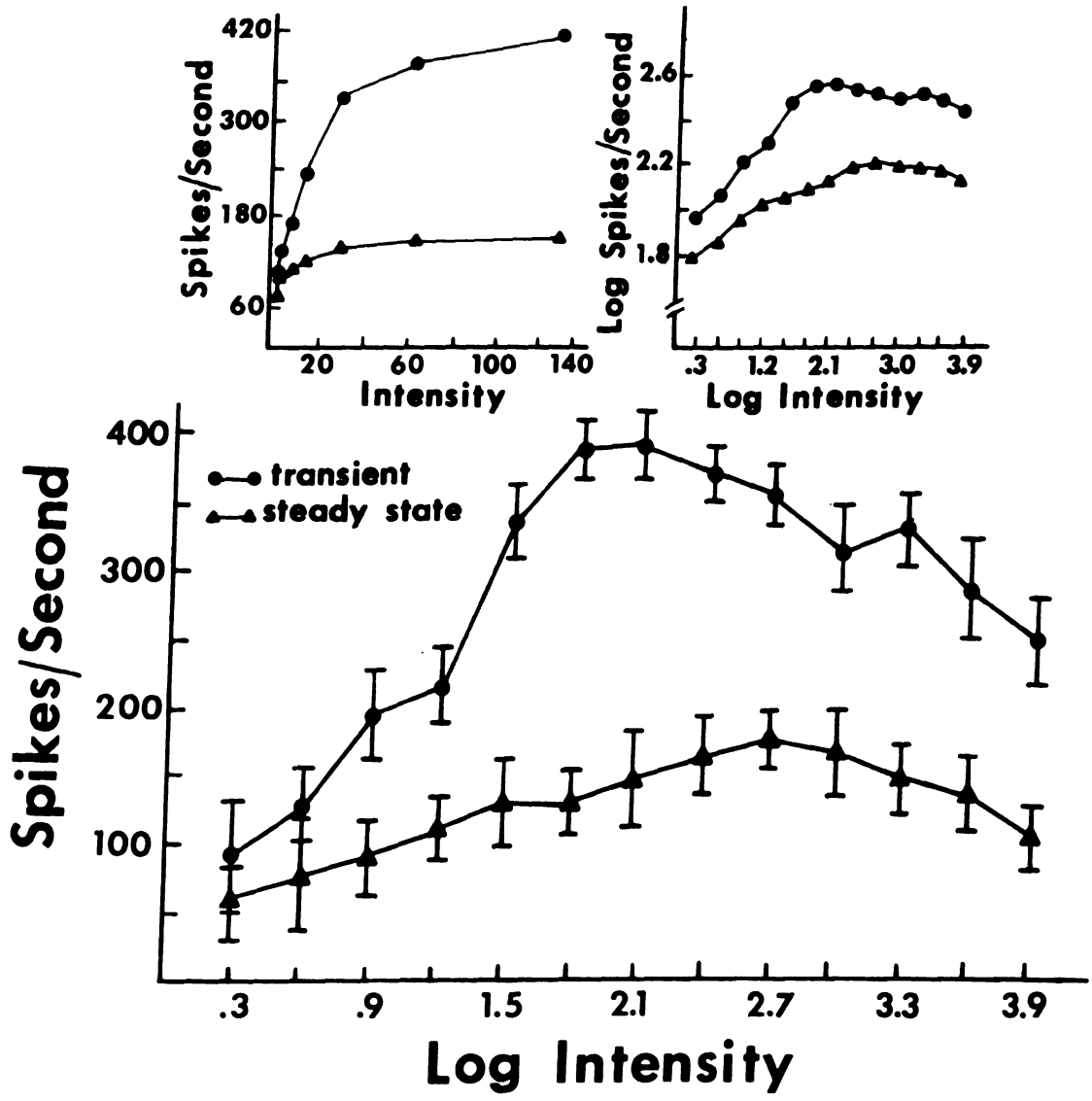
420
300
180
60
Spikes/Second
20
60
100
140
Intensity
2.6
2.2
1.8
Log Spikes/Second
.3
1.2
2.1
3.0
3.9
Log Intensity
400
300
200
100
Spikes/Second
transient
steady state
.3
.9
1.5
2.1
2.7
3.3
3.9
Log Intensity

Figure 4

with a mean length of 2.1 log units (S.D. = .67) for the transient phase and 2.3 log units (S.D. = .79) for the steady state phase. In most cases non-monotonic decreasing relationships were found for the high contrast portion of the curve. Three cells had functions for the transient component which came to an asymptote at about 2.1 log units above threshold; two other cells showed a similar effect for the steady state component. The peak firing rate of the transient component was usually about 3 times greater than the peak firing rate for the steady state component. The slopes (on a semilog plot) of the rising portion of the curves were analyzed and found, in general, to be about four times greater for the transient component. Table 1, which is shown in a latter part of the Results section, gives a more detailed account of the slope analysis.

Spot size variation had the effect of changing the threshold intensity without significantly altering the shapes of the suprathreshold stimulus-response functions. This was found to be true for both the transient component curves (Figure 5) and the steady state component curves (Figure 6).

Following the pattern of the spots shown in the two figures, the stimulus-response functions for most spots showed the previously mentioned monotonic increasing portion for low contrast stimuli and the non-monotonic

Figure 5.--Transient component stimulus-response functions for an on-center cell. Numbers on the abscissa are neutral density filter values (higher densities represent lower intensities). The first point, i.e., the one closest to the vertical axis, on each function corresponds to threshold intensity. Right eye unit whose receptive field was located 10° nasal and 4° superior to the area centralis; receptive field center size = 3.2°; background light = 1 log candle/m^2.

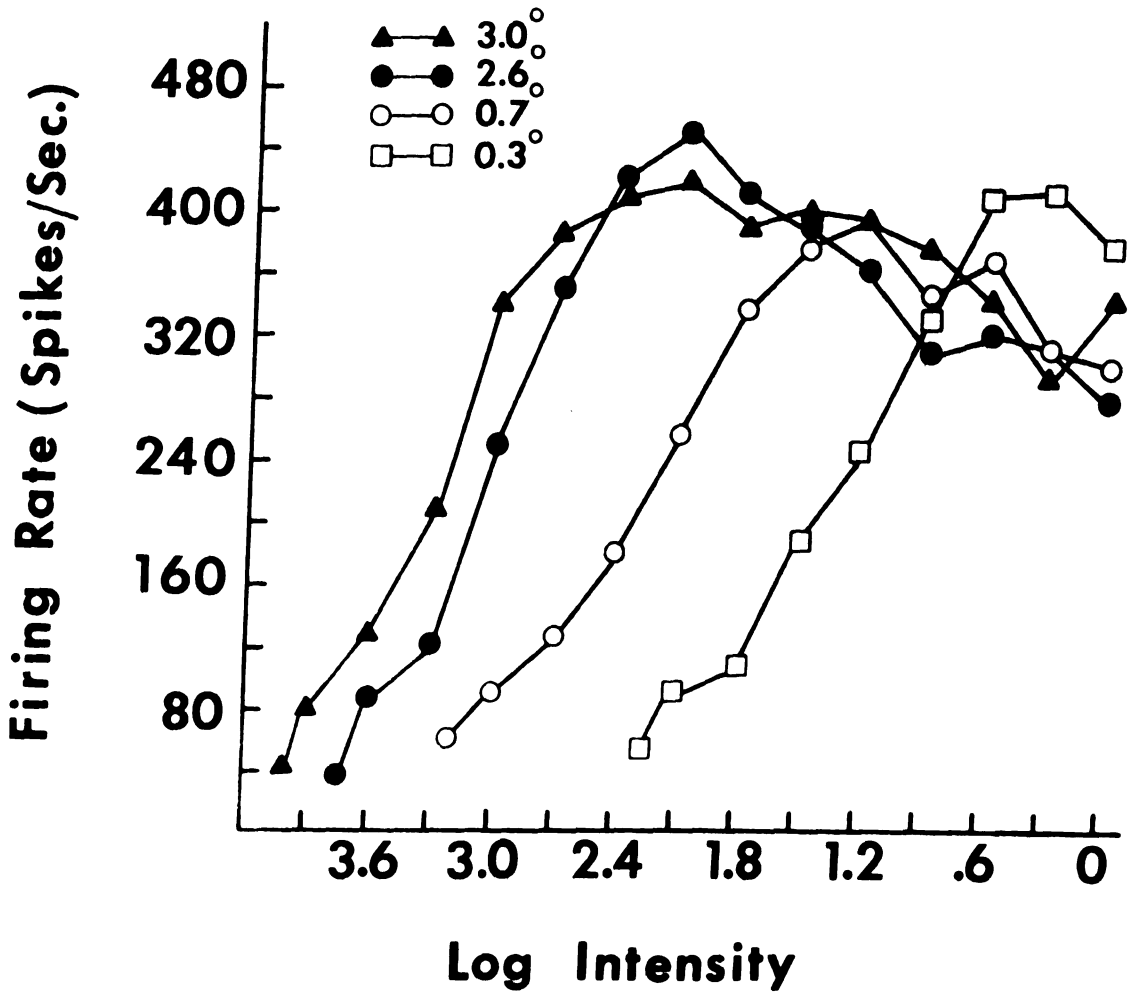
3.0°
2.6°
0.7°
0.3°
480
400
320
240
160
80
Firing Rate (Spikes/Sec.)
3.6
3.0
2.4
1.8
1.2
.6
0
Log Intensity

Figure 5

Figure 6.--Steady state component stimulus-response functions for an on-center cell. Numbers on the abscissa are neutral density filter values. The first point on each function corresponds to threshold intensity. Right eye unit whose receptive field was located 11° nasal and 3° inferior to area centralis; receptive field center size = 4.5°.

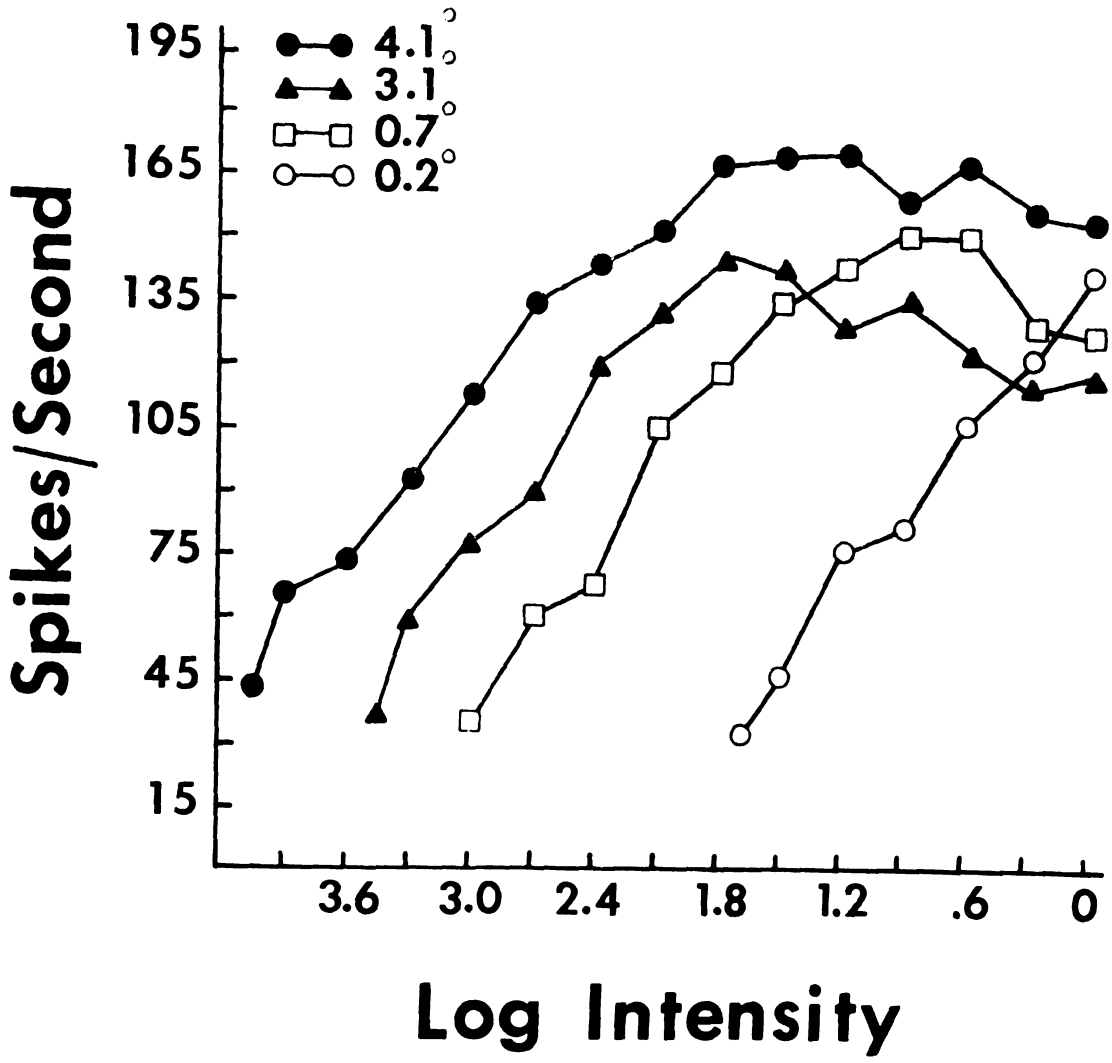
195
165
135
105
75
45
15
Spikes/Second
4.1°
3.1°
0.7°
0.2°
3.6
3.0
2.4
1.8
1.2
.6
0
Log Intensity

Figure 6

decreasing portion for the high contrast stimuli, with a change in tonicity occurring at about 2.2 threshold units. Although the peak firing rates for various spot sizes differed by as much as 70 spikes per second for the transient component curves and 30 spikes per second for the steady state component curves, the differences did not follow any systematic pattern. For some cells the small spots showed the highest firing rate; for others the larger spots showed higher peak responses. In most cases the differences in peak firing rates were minimal. An F test for homogeneity of regression[2] (Winer 1962) was performed for the monotonic, i.e., low contrast portion, for the transient component curves (8 cells) and for the steady state curves (8 cells) of 16 on-center cells. In all 16 cases non-significant F values ($p < .10$) were obtained, thus indicating that the slopes of the least squares straight lines could not be distinguished statistically. Systematic differences in the amount of high contrast decline were also difficult to find. Thus, in general, statements made regarding the differences between the transient and steady state functions, i.e., slope, peak firing rate, and point of tonicity change, can be made

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[2]This is typically used in an analysis of covariance to test the null hypothesis that the population coefficients of linear regression are equal. Thus, significant F values would indicate differences in the slopes of the least squares lines.

for any sized spot (used in this study) which primarily activated the central region of the receptive field.

Although their effects were not systematically examined, spots which were large relative to the size of the receptive field center, e.g., a 7° spot covering a receptive field with a 2° center, resulted in irregular stimulus-response relationships with very limited ranges of monotonicity. The slopes of the low contrast portion of such curves were usually more gradual than those found for smaller spots.

The average response histograms in Figure 7 disclose other differences in the effects of low and high contrast stimuli. For low contrast levels the histograms were shaped like the ones first reported by Rodieck and Stone (1965). The major effect of increasing luminance was to increase the magnitude of the on response. The time constants of decay for the transient component, which remained relatively stable for low contrast stimuli, were usually between 35 and 45 msec. At the termination of the stimulus the firing rate dropped to zero before returning to the maintained level.

The histograms for high contrast stimuli differed markedly from those for low contrast stimuli. The magnitude of the on response was found to decrease, rather than increase, with increases in luminance. The decay from the peak of the transient component became

Figure 7.--Average response histograms for an on-center cell. Histograms have been traced from oscilloscope photographs taken from the "y" axis output of the C.A.T. (bin width = 5 msec.). Smoothing has concealed small changes--less than 5 per cent--in firing rate. Values on the "z" axis are in log units above threshold; the pulse length is 920 msec. For luminance levels up through 2.1 threshold units the firing rate drops to zero at the termination of the stimulus pulse; it does not drop to zero for levels above 2.1 threshold units. Peak firing rates, during transient phase are: .9 - 397, 1.5 - 596, 2.1 - 710, 2.7 - 653, 3.3 - 590, 3.9 - 482. Spot size = 0.6° for right eye unit with receptive field center size of 1.2°, located 5° nasal and 12° superior to area centralis.

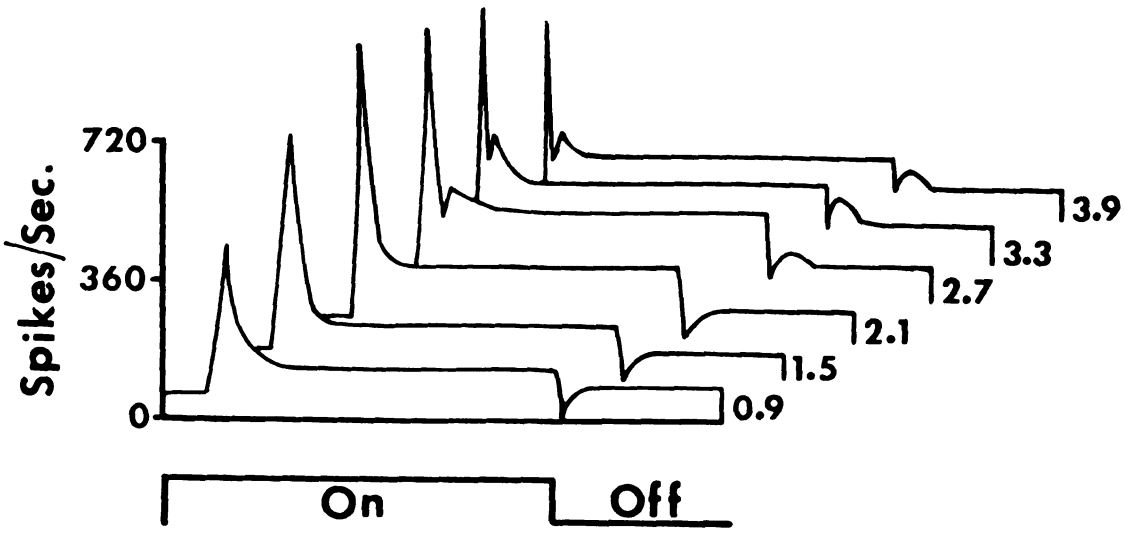

Figure 7

progressively more accelerated with time constants of decay reaching as low as 10 msec. This rapid decay was followed by a second rise in response magnitude.[3] The maximum firing rate during this phase, which was as high as 250 spikes per second, occurred 35-55 msec. after stimulus onset. Its magnitude decreased in a non-monotonic fashion with increases in luminance.

Although the firing rate decreased immediately following the termination of the stimulus, it rarely dropped to zero. Off responses were usually present at high contrast levels with their firing rates reaching as high as those during the steady state component of the on response. The strength of the off response increased non-monotonically with increases in luminance.

Latency changes also accompanied increases in intensity. For a stimulus .3 log units above threshold, the highest firing rate, i.e., the peak of the transient component, occurred about 50 msec. after the onset of the stimulus. As intensity was increased the latency of the response became progressively shorter until, at

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[3]The term "transient component" has been used in this paper to refer to the portion of the response in which the rate of change of firing rate is high. In a similar way the term "steady state component" has been used to refer to the phase where the rate of change of firing approaches zero. The second rise in firing rate observed for high contrast stimuli, therefore, was considered as a part of the transient component and was included in the measurements of its magnitude.

about 2.4 threshold units, the peak firing rate occurred at about 5 msec. after stimulus onset. The latency remained at this level for high contrast stimuli. Figure 8 shows this effect in a more detailed form.

Off-Center Cells.--Figure 9 reveals that there were both similarities and differences between stimulus-response relationships for on-center and off-center cells. As in the case of on-center cells, the stimulus-response functions could be divided into low and high contrast segments. The low contrast component was usually monotonic increasing with a mean length of 2.2 threshold units (S.D. = .61) and looked very similar to the corresponding portion for on-center cells. High contrast stimuli were found to be more suppressive for off-center cells than for on-center cells. It was not uncommon to observe firing rates for this intensity range which were as low as the maintained firing level. None of the on-center cells studied showed this amount of decline in response magnitude. The variability of the response magnitude (as measured by confidence intervals) for high contrast stimuli was found to be greater for off-center cells than for on-center cells.

Manipulation of spot size had minimal effects upon the shapes of the stimulus-response functions of off-center cells (Figure 10). Marked high contrast suppression was observed for most spots which primarily

Figure 8.--Latency changes for an on-center cell. Numbers on the abscissa are expressed as log units above threshold. Ordinate values refer to the latency, in msec., of the peak of the transient component. Spot size = 1.8° for left eye unit with receptive field center of 2.2°, located 6° temporal and 11° inferior to the area centralis. Background intensity = 0 log candles/m^2.

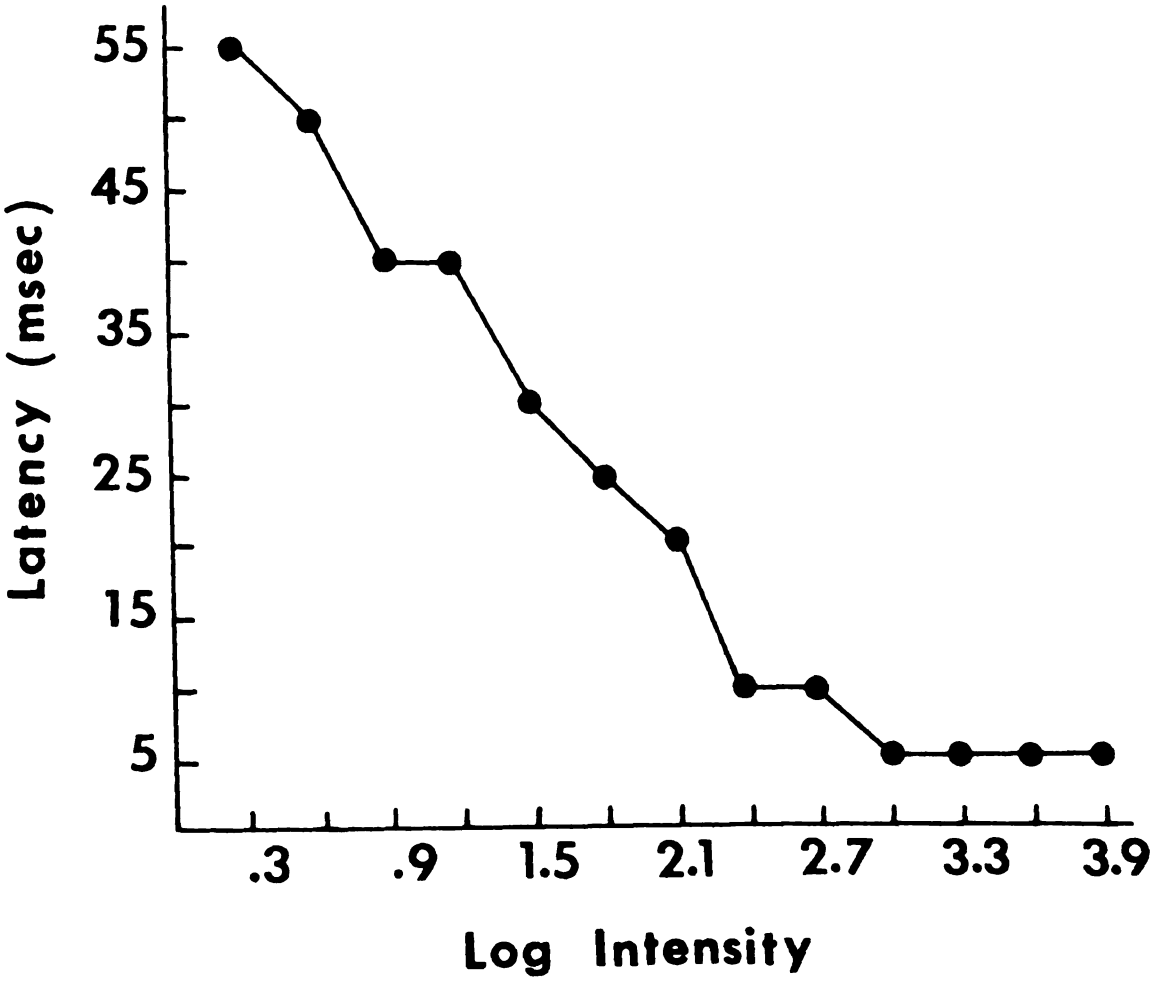

Figure 8

Figure 9.--Stimulus-response function for transient component of an off-center cell. Numbers on abscissa are in log units above threshold. Bars around points are 99 per cent confidence intervals. Spot size = 1.0°, for right eye unit with receptive field center size of 2.5°, located 5° nasal and 2° superior to the area centralis. Background intensity = 0 log candles/m^2.

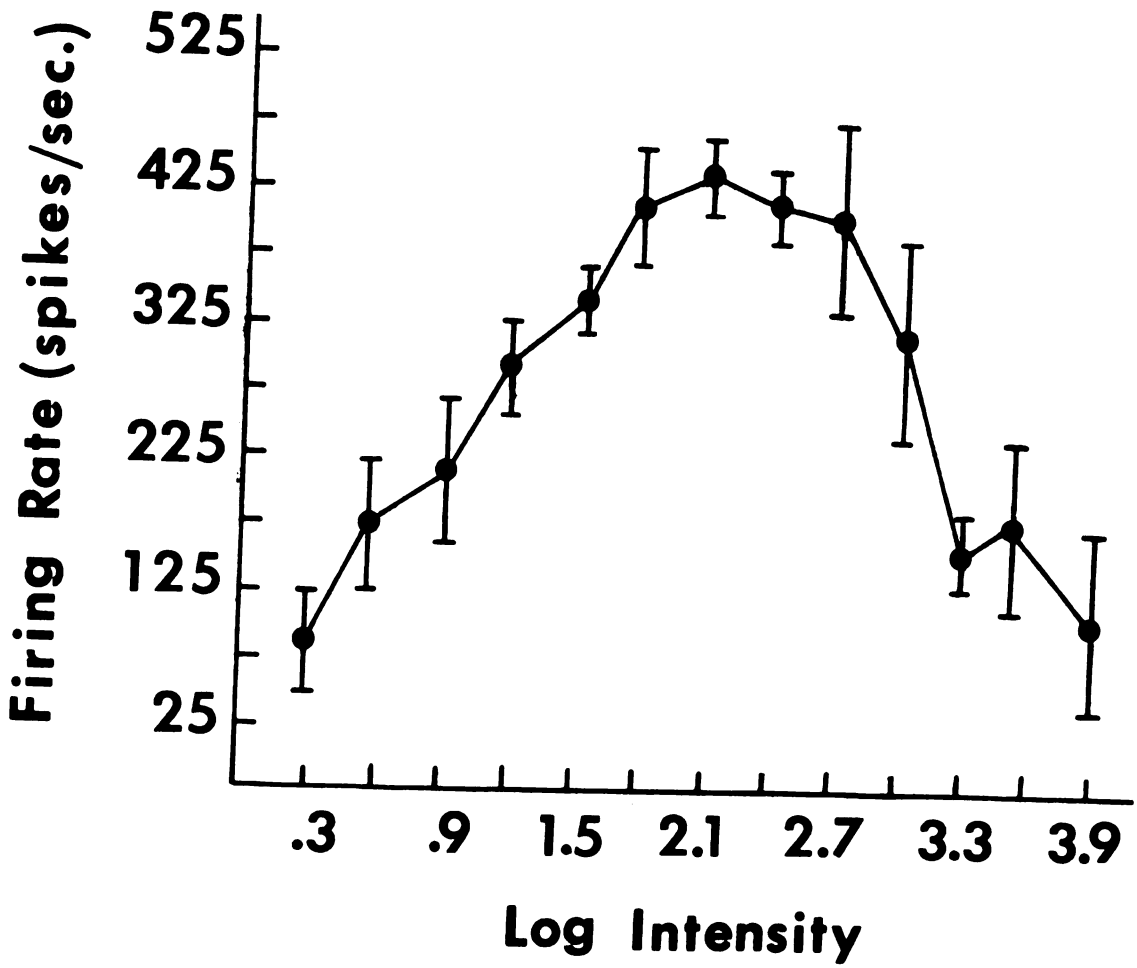
Firing Rate (spikes/sec.)
525
425
325
225
125
25
.3
.9
1.5
2.1
2.7
3.3
3.9
Log Intensity

Figure 9

Figure 10.--Stimulus-response functions for transient component of an off-center cell. Numbers on the abscissa are neutral density filter values. Reading from left to right, the first point on each function represents threshold intensity. Right eye unit with receptive field center of 3.5°, located 1° nasal and 14° inferior to the area centralis. Background intensity = 1 log candle/m^2.

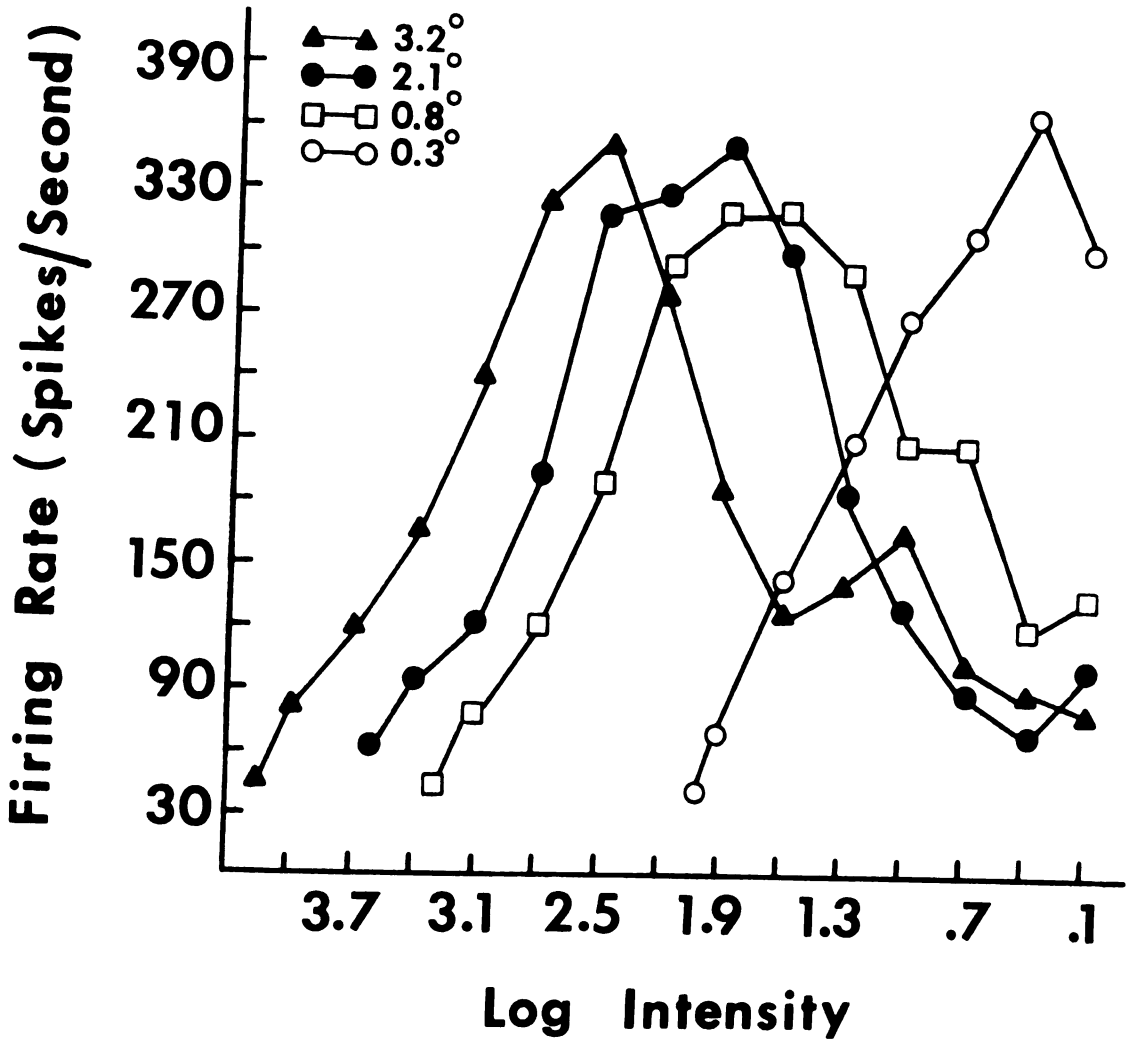
Firing Rate (Spikes/Second)
390
330
270
210
150
90
30
3.2°
2.1°
0.8°
0.3°
3.7
3.1
2.5
1.9
1.3
.7
.1
Log Intensity

Figure 10

activated the central region of the receptive field, i.e., that were not large relative to the size of the receptive field center. An F test for homogeneity of regression for the monotonic portion of the transient curves was made for eight off-center cells. The non-significant F values, ($p < .10$) found in all eight cases indicate, as in the case of on-center cells, that the shapes of the rising portions of the curves were not, from a statistical standpoint, discriminable. In general, the conclusions made for on-center cells regarding the effect of spot size variation could also be made for off-center cells.

The average response histograms shown in Figure 11 illustrate the effect of luminance variation upon the time course of the response of a typical off-center cell. For low contrast levels the shape of the off response remained relatively constant for the various luminance levels. As was the case for the on response for on-center cells, the magnitude of the off response increased in proportion to luminance. Many of the high contrast effects that were found for on-center cells were also observed for off-center cells: the peak of the transient component showed an accelerated decay; a second rise in firing rate occurred; and the overall magnitude of the response decreased with increases in luminance. Although off responses were quite common for on-center cells, on responses (which would be analogous) were rarely observed

Figure 11.--Average response histograms for an off-center cell. Histograms were traced from oscilloscope photographs. Smoothing has concealed small (less than 5 per cent) changes in firing rate. Numbers on "z" axis are log units above threshold. Peak firing rates are: .9 - 240, 1.5 - 408, 2.1 - 600, 2.7 - 432, 3.3 - 288, 3.9 - 192. On responses were not observed for this unit. Spot size = 1° for left eye unit whose receptive field center was 2° in diameter, located 5° temporal, and 2° inferior to the area centralis. Background intensity = 1 log candle/m^2.

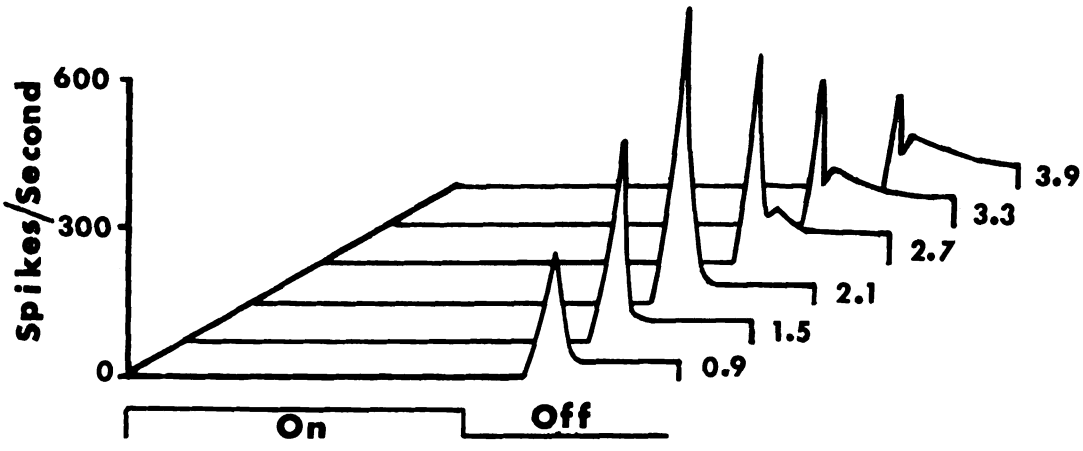

Figure 11

for off-center cells. Decreases in latency were small--usually less than 20 msec--in comparison to on-center cells.

Best Fit Analysis

Using a least squares criterion, logarithmic ($R = a \log_{10} S$), power ($R = bS^n$) and linear ($R = cS$) functions were fitted to the low contrast data[4] for ten on-center and ten off-center cells. A medium sized spot, e.g., a 1° spot in a field whose center was 2° in diameter, was examined for each of the twenty cells. Stimulus magnitudes were expressed in threshold units; response magnitudes as the difference between observed and maintained (spontaneous) firing rate. A linear regression model was employed in the analysis of each of the three functions. A straight line was fitted to the data plotted on linear coordinates to test the accuracy of the linear prediction rule; to test the log function it was fitted to the data plotted on semilog coordinates; and for the power function, to the log-log data. Employing the theory of linear regression enabled the use of the Pearson product-moment correlation coefficient as a measure of

[4]From a statistical standpoint a linear regression model may not be applicable to the high contrast data because the curves were generally non-monotinic, i.e., there may be non-linear components.

the goodness of fit. A "t" test for zero linear regression (Walker and Lev 1953) was also made.

As can be seen from Table 1, the values of the Pearson product-moment correlation coefficients were usually lower for the linear function than for either of the negatively accelerated functions. Of the 20 cells studied, only one showed a statistically significant value of $\underline{r}$ for a linear function whereas, highly significant correlation coefficients were found in all but two cases for the log and power relations. The mean $\underline{r}$ values for the 20 cells were above .90 for both log and power relationships, with individual cells often showing values as high as .98. Although these data indicate that the shapes of the transient and steady state component curves were very similar, it also shows that their slopes differed markedly. On the average, the slope, for the semilog data, was about four times greater for the transient component curves. This difference in rate of rise is also reflected in the difference in exponents for the power function.

Table 1.--Summary of best fit analysis for power, logarithmic and linear functions.

Unit (on center)	Power $R=aS^n$				Logarithmic $R=b \log_{10} S$				Linear $R=cS$	
	Transient		Steady State		Transient		Steady State		Transient	Steady State
	r	n	r	n	r	slope	r	slope	r	r
1	.97**	.42	.94**	.31	.98**	191	.94**	56	.78	.81
2	.87*	.48	.89*	.30	.98**	205	.96**	45	.72	.78
3	.88*	.51	.95**	.40	.91*	210	.91*	68	.79	.76
4	.96**	.32	.89*	.24	.92*	180	.98**	47	.76	.81
5	.89*	.47	.89*	.38	.96**	199	.96**	69	.80	.72
6	.88**	.45	.90*	.30	.97**	197	.91*	46	.81	.70
7	.98**	.46	.94**	.34	.96**	221	.90*	66	.76	.75
8	.87*	.35	.92*	.24	.87*	186	.84	60	.71	.79
9	.89*	.31	.86*	.21	.89*	185	.90*	44	.73	.81
10	.92*	.32	.91*	.26	.89*	181	.91*	46	.78	.82
mean	.91	.40	.90	.29	.93	196	.93	55	.76	.77

Table 1.--(Continued)

Unit (off center)	Power $R=aS^n$				Logarithmic $R=b \log_{10} S$				Linear $R=cS$	
	Transient		Steady State		Transient		Steady State		Transient	Steady State
	r	n	r	n	r	slope	r	slope	r	r
1	.98**	.40	---	---	.91*	220	---	---	.79	---
2	.91*	.47	---	---	.96**	206	---	---	.81	---
3	.86	.41	---	---	.98**	184	---	---	.81	---
4	.89*	.30	---	---	.94*	187	---	---	.83	---
5	.92*	.29	---	---	.90*	194	---	---	.74	---
6	.97**	.36	---	---	.96**	216	---	---	.79	---
7	.95**	.34	---	---	.98**	176	---	---	.78	---
8	.90*	.38	---	---	.93*	194	---	---	.76	---
9	.89*	.36	---	---	.88*	189	---	---	.88*	---
10	.87*	.54	---	---	.89*	203	---	---	.77	---
mean	.90	.39	---	---	.93	197	---	---	.79	---

n - exponent for power function.
r - Pearson product-moment correlation coefficient.
slope - least square slope for semilog plot.
* - $p(t) < .01$
** - $p(t) < .001$

DISCUSSION

High Contrast Effects

Several investigators (Brown and Wiesel 1959, Cleland and Enroth-Cugell 1968, Steinberg 1969, Stone and Fabian 1968) have reported, in a semiquantitative manner, that high contrast stimuli have suppressive effects upon the activity of cat retinal ganglion cells. The results of the present study are consistent with these reports but also show: (1) that high contrast suppression occurs for both the transient and steady state responses of on-center cells; (2) that the suppressive effect is more pronounced for off-center cells than on-center cells; (3) that it occurs for a wide range of spot sizes.

Spatial Summation at Threshold

Area-threshold relationships for cat retinal ganglion cells have been studied by Barlow et al. (1957) and Wiesel (1960) but most extensively by Cleland and Enroth-Cugell (1968). In the Cleland and Enroth-Cugell study, area-threshold curves for on-center cells were determined with sinusoidally modulated stimuli. Thresholds were found to first decrease, then level off, as

spot size was increased. The change in slope occurred as spot diameter reached that of the receptive field center. Although some of the cells encountered in the present study showed slight increases in threshold at the edge of the receptive field center, the shapes of the functions, were, for the most part, like those reported by Cleland and Enroth-Cugell. Barlow et al. (1957) and Wiesel (1960), who both used square wave stimuli, reported that many of the cells they studied showed "U" shaped functions, where thresholds were found to rise sharply at the border between the center and the surround of the receptive field. These results are difficult to reconcile with those of the present study.

Cleland and Enroth-Cugell also determined the best fitting straight line for their area-sensitivity (reciprocal threshold) data plotted on log-log coordinates. A line with a slope of two, which is the slope predicted by Ricco's law (area x intensity = constant) for data graphed in this manner, (The slope for a graph of the data of the present study would have a slope of about 1.45 if displayed in this way; Piper's law would predict a slope of +1.) was found to be the best linear prediction rule for the increasing portion of the function, i.e., for spots which did not invade the surround. The rate at which threshold fell with increasing spot size was found, in the present study, to be more gradual

than this. The slope of the best fitting straight line was found to lie between the ones predicted by Ricco's and Piper's ($\sqrt{\text{area}}$ x intensity = constant) law. Perhaps the difference in the wave shape of the stimuli used in the two studies, i.e., sine wave versus square wave, accounts for the disparity in the results. Unfortunately, neither Barlow et al. (1957) nor Wiesel (1960) analyzed their data in this manner.

Spatial Summation for Supra-threshold Stimuli

In examining the stimulus-response functions for a variety of spot sizes, one cannot avoid noticing the similarity of their shapes. The likeness of the functions becomes even more apparent if the stimulus magnitudes are described in threshold units. All of the functions, for a given cell, change from an increasing to a decreasing portion at about 2.2 threshold units; this change usually occurs at about the same response magnitude; and the suppression of the response that occurs for subsequent, high contrast, luminance levels is of the same order of magnitude for all of the spots. The negative results of the homogeneity of regression analysis suggest that the slopes of the rising phase of the functions cannot, from a statistical standpoint, be

distinguished.[5] This latter finding points out an even more important aspect of the suprathreshold data. It suggests, in the form of a testable hypothesis, that cat retinal ganglion cells show linear spatial summation for low contrast levels. It is also reasonable to hypothesize that the magnitude of the suprathreshold summation is equal to the summation found at threshold. An example will serve to illustrate this point. Suppose that an experiment were conducted on a cell in which the rising portions of the stimulus-response functions for a number of spots (which activated only the central region of the receptive field) had exactly the same slope. Suppose, also, that in the experiment on this cell, a suprathreshold response criterion, of say 150 spikes/second were chosen and the intensity of various spots was varied until this firing rate was reached for each spot. If the same procedure was repeated for a number of response criteria, according to the hypotheses, one should find functional relationships between spot size and intensity (for a constant response) which are essentially the same. This function should be similar to the one found for threshold

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[5]It cannot be stated that the population slopes are equal since this would require accepting the null hypothesis--an inexcusable act. The argument is still statistically well founded, however, because non-significant $\underline{F}$ values were obtained for 24 cells, i.e., the probability of making a type I error decreases when results are repeatable.

stimuli which activated only the central region of the receptive field, i.e., increasing spot size should result in a decrease in the intensity necessary to reach the criterion response. The slope of the line depicting these data should have a value of approximately -1.45 for all response criteria associated with low contrast stimuli. (See Figure 12)

Intensity Code

Perhaps the most salient feature of the stimulus-response functions is the difference in the shape of their high and low contrast portions. These differences are very significant from the standpoint of cells in higher visual centers, like the lateral geniculate nucleus, which receive information from retinal ganglion cells. When intensity is increased in the low contrast range, the picture presented by the retinal ganglion cell is quite clear: an increase in luminance, within limits, is signalled by an increased firing rate. The picture given in the high contrast range, on the other hand, is quite different. Sometimes an increase in firing rate results from an increase in luminance; at other times a decrease in firing rate occurs. The amount of change in response magnitude per incremental increase in intensity, is at least for on-center cells, much smaller for high contrast levels than for low ones. Although the increments

Figure 12.--Theoretical area-constant response curves plotted on log-log coordinates. Abscissa and ordinate units are arbitrary but logarithmically spaced. The higher curves represent higher response criteria. All curves have slopes equal to -1.45.

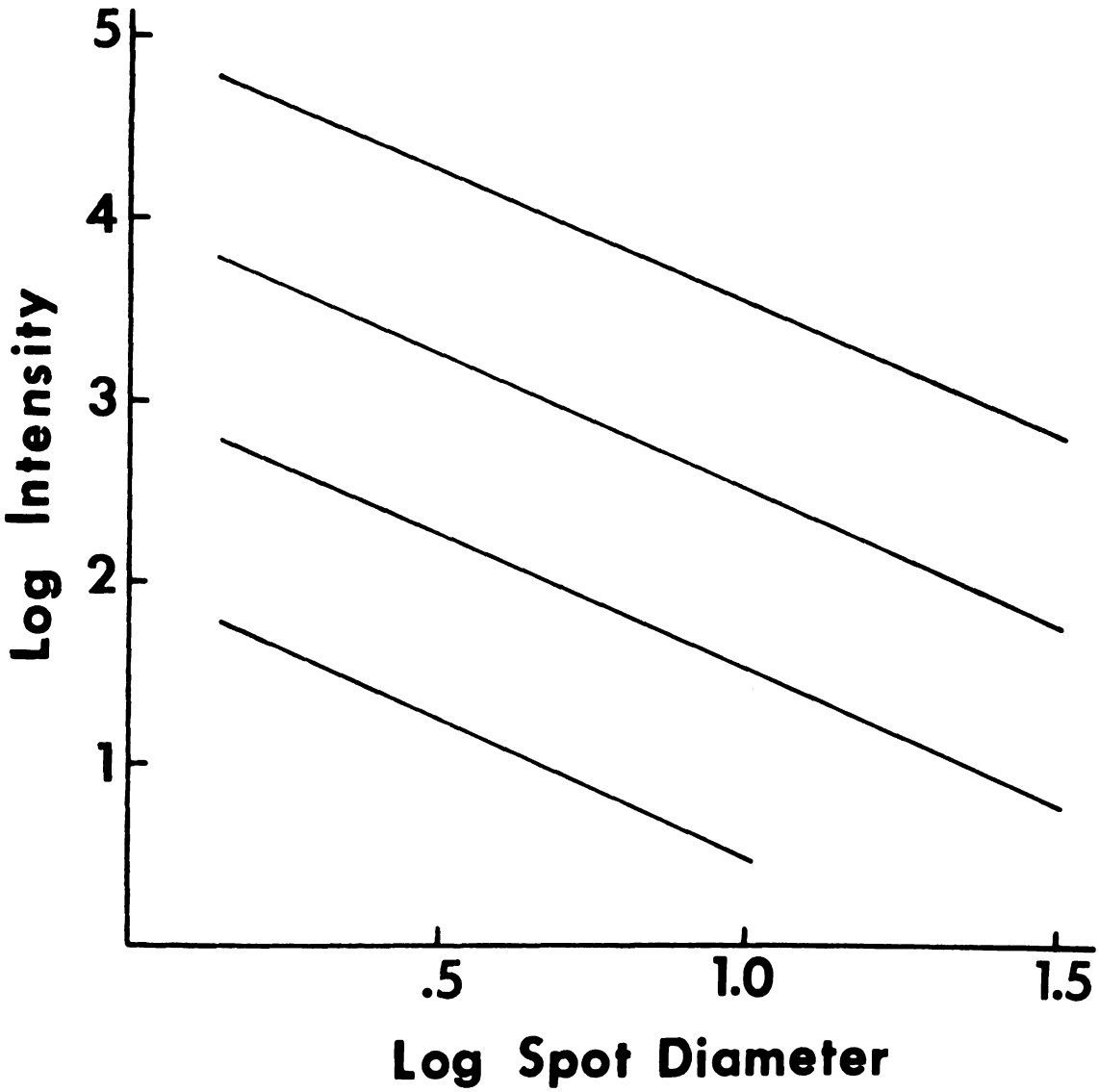

Figure 12

in firing rate are about the same for both ranges in the case of off-center cells, the variability in response magnitude is much greater for the high contrast stimuli. Apparently, cat retinal ganglion cells are designed to give a more precise representation of changes in luminance for the low contrast range. From a functional standpoint this is not an unexpected finding, since luminance differences greater than two log units are rarely encountered in the cat's normal environment. One would expect, therefore, that these cells would have a more precise intensity code in the contrast range in which they normally function.

Several investigators (DeValois 1965, Easter 1968, Stone and Fabian 1968) have attempted to determine the mathematical relationship which gives the best approximation of stimulus-response functions (over monotonic ranges) found for single cells of vertebrate visual systems. Using diffuse achromatic stimuli DeValois (1965) determined stimulus-response relationships for rhesus monkey lateral geniculate (broad band) cells. He reported that monotonic relationships could only be found over one log unit intensity ranges. Although it was concluded that either a logarithmic or power function adequately depicted the data for this range, this was not substantiated with statistical tests.

Perhaps the most comprehensive study related to this question was conducted on retinal ganglion cells in the goldfish retina (Easter 1968). Easter varied the intensity, over restricted ranges, of brief (10 msec.) monochromatic spots (620 nm) presented in the central region of "red, on-center" cells. His statistical analysis unequivocally demonstrated a non-linear intensity code. A power function with an exponent of .5 was found to be superior to other negatively accelerated functions that were examined.

Stone and Fabian (1968) pooled low contrast stimulus-response data from ten cat retinal ganglion cells and examined the goodness of fit of logarithmic, power, and linear functions. Only the peak firing rates of the transient component were analyzed and both stimulus and response values were measured as percentages of the maximum values encountered. The Pearson product-moment correlation coefficients they reported for the logarithmic, power and linear function were .94, .86, and .80, respectively. They concluded that stimulus-response relationships were non-linear.

The results of the statistical analysis in the present study also indicate a non-linear intensity code for cat retinal ganglion cells. Correlation coefficients for a linear function, which were usually lower than .80, fell below the .01 significance level for 19 of the 20

cells studied. On the average, only about 60 per cent of the variance could be accounted for by this type of relationship. In marked contrast to this, both of the negatively accelerated functions that were examined showed highly significant Pearson product-moment correlation coefficients. On the average about 80 per cent of the variance could be accounted for by employing either a logarithmic or power function.

Analyzing the transient and steady state components separately revealed another important point about intensity coding mechanisms. Although the rising portions of both have essentially the same shape, they differ markedly in slope. The slope of the least squares straight line fitted to the semilog data, on the average, was found to be four times greater for the transient component functions. The firing rate at the peak of the functions was usually three to four times greater for the transient component functions and for brief, 5 msec. intervals, as much as five times greater. In general, it took a much larger increment in intensity to produce a reliable change in firing rate for the steady state component than for the transient component. From a functional standpoint, then, the most information about intensity would be gained by the cat when there is a great deal of movement, either of its eyes or of the visual target. In this way illumination would be constantly entering the receptive fields of

on-center cells and leaving the receptive fields of off-center cells, thereby constantly causing transient bursts of neural activity.

Mechanisms

According to Rodieck and Stone (1965), cat retinal ganglion cell activity is controlled by excitatory and inhibitory processes. The relative contribution of these two influences is dependent upon the portion of the receptive field activated and the type of cell, i.e., on-center or off-center. For on-center cells, the excitatory process is more influential when luminous spots are presented in the central region of the receptive field. For off-center cells, inhibitory effects predominate under these conditions. The process which was found to be most influential for spots placed in the center of the receptive field was referred to by Rodieck and Stone as the "center mechanism." In a similar way, the less-influential process was referred to as the "surround mechanism." Thus for on-center cells, the excitatory process was called the center mechanism and the inhibitory process was referred to as the surround mechanism; the terms are reversed for off-center cells. The onset of the surround mechanism, according to Rodieck and Stone (1965), occurs about 50 msec. after the onset of the center mechanism when low contrast stimuli are used. (See Figure 13)

Figure 13.--Receptive field model (reproduced from Rodieck and Stone, 1965). The dome shaped curves at the top depict the strength of the center and surround mechanisms at different positions in the receptive field. Also shown is the time course of the center and surround mechanisms for three positions in the receptive field of an on-center cell. For the position closest to the center of the field the excitatory process predominates. The strength of the center and surround mechanisms are approximately equal at the second position. If their time of onset were the same, no response would be observed. If the surround mechanism is delayed by about 50 msec., however, on-off responses occur--the type of responses actually observed in their experiment. The surround mechanism predominates in the third position.

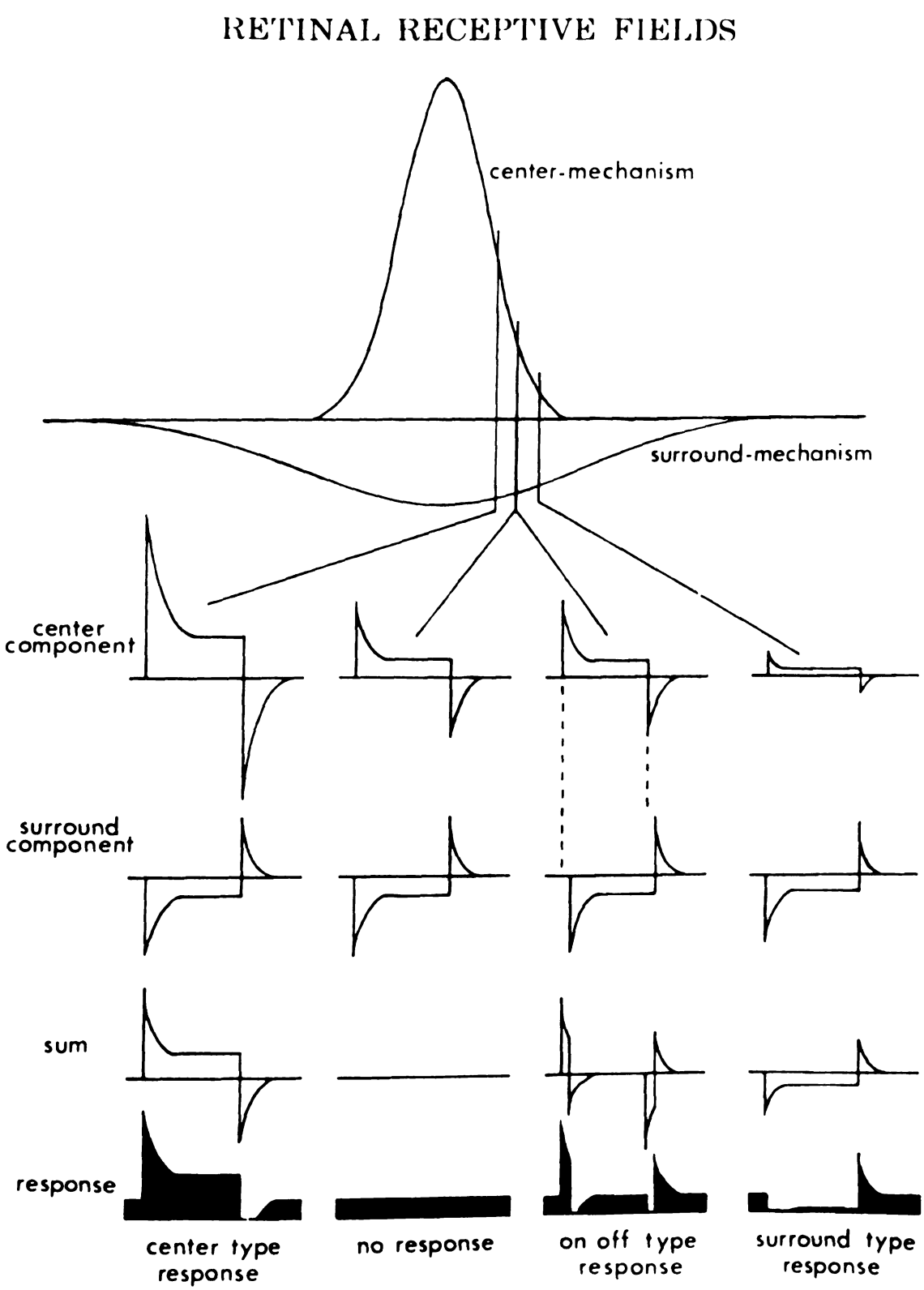
RETINAL RECEPTIVE FIELDS
center-mechanism
surround-mechanism
center component
surround component
sum
response
center type response
no response
on off type response
surround type response

Figure 13

It seems reasonable to assume, in accordance with the Rodieck and Stone model, that increasing luminance over the low contrast range had the effect of increasing the magnitude of both the excitatory and inhibitory influences upon the ganglion cell, with the inhibitory effects predominating for off-center cells and the excitatory effects predominating for on-center cells. Presumably, the slope of the transient component curves are much greater than the steady state component curves because the onset of the surround mechanism occurs about 50 msec. after the onset of the center mechanism. That is to say, the steady state component represents the sum of both excitatory and inhibitory influences whereas the transient component, for the most part, reflects excitatory inputs for on-center cells and inhibitory inputs for off-center cells. As the intensity enters the high contrast range the data suggest that two things occur: (1) the surround mechanism's relative strength, i.e., relative to the center mechanism, increases; (2) the temporal relationship between the onset of the center and surround mechanism changes; their time of onset is about the same for high contrast stimuli. The rationale for the necessity of <u>both</u> of these conditions is as follows. If condition (1) were true and condition (2) were false, the steady state component would have shown high contrast suppression and the transient component would have kept rising in strength. If

condition (2) were true but condition (1) false, the transient component would have shown high contrast suppression and the steady state component would not have. Although transient and steady state components could not be compared for off-center cells, there is no reason to argue that these assumptions do not apply to them also. One can account for the major difference between the effect of luminance upon the two cell types, i.e., that there was greater high contrast suppression for off-center cells, by making the additional assumption that the increase in the relative strength of the surround mechanism is greater for off-center cells. (See Figure 14)

One might ask what anatomical structures and neurophysiological events in the retina underlie the mechanisms that have been proposed. A receptive field model presented by Rodieck (1967a) gives a reasonable answer to this question. According to this model receptor activation in any part of the receptive field has the immediate effect of increasing bipolar cell activity. It is presumed that bipolar cells form both presynaptic and postsynaptic connections with amacrine cells; they excite amacrine cells, but, in turn, are inhibited by these same cells, thus providing a means of lateral inhibition. Amacrine cells and bipolars have opposite effects on ganglion cells. The effect depends upon the cell type: for on-center cells, bipolar cells are

Figure 14.--Schematic of mechanisms proposed to account for observed stimulus-response functions. For low contrast stimuli the center mechanism predominates and leads the surround mechanism by about 50 msec. The relative strength of the surround mechanism, especially for off-center cells, increases at high contrast levels. The latency of both mechanisms decreases but the latency differential between them disappears.

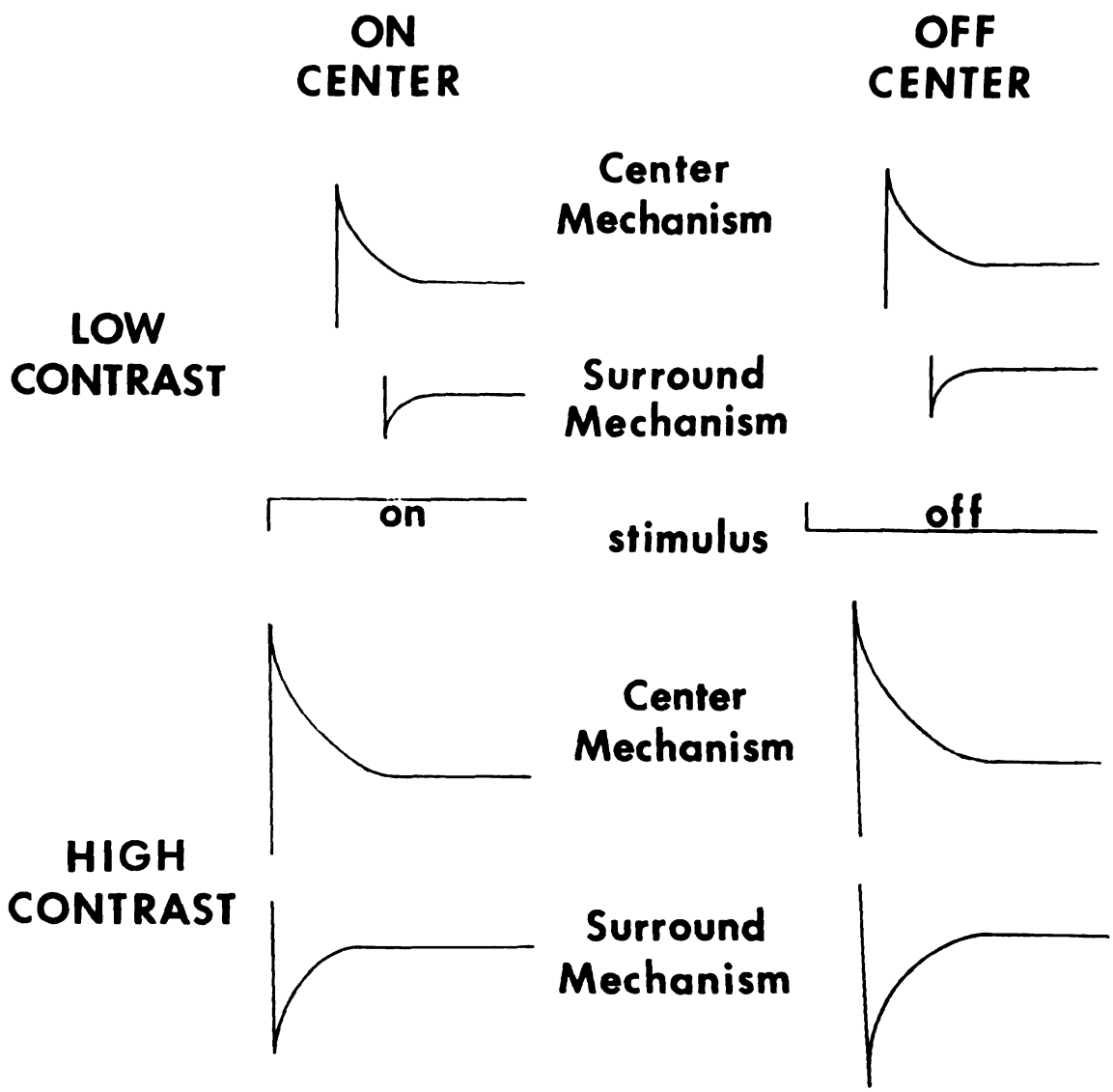
ON
CENTER
OFF
CENTER
Center
Mechanism
LOW
CONTRAST
Surround
Mechanism
on
stimulus
off
Center
Mechanism
HIGH
CONTRAST
Surround
Mechanism

Figure 14

excitatory and amacrine cells are inhibitory; for off-center cells, amacrine cells are excitatory and bipolar cells are inhibitory. When illumination causes activation of both bipolar cells and amacrine cells, the effect of bipolar cells predominates. (See Figure 15)

Let us now consider the neurological events that might occur under the conditions of the present experiment. Presenting a luminous spot in the center of the receptive field would lead to receptor activation, then to increased activity in the bipolar cells. Bipolar cells would excite amacrine cells, which in turn, would inhibit bipolars. For on-center cells, the amacrine cells would inhibit and the bipolar cells would excite, the ganglion cells to which they both make connections. The opposite would occur for off-center cells. For on-center cells the excitatory influences would predominate for all luminance levels and for off-center cells the inhibitory influence would predominate. One could explain the difference in the slope of the transient and steady state components curves by simply assuming that the amacrine cell effects are delayed by about 50 msec. at low contrast levels. High contrast suppression could be explained by presuming that amacrine cell effects are relatively greater for high contrast stimuli. One would also have to presume that these effects are no longer delayed and that they are greater in magnitude for off-center cells than for on-center cells.

Figure 15.--Rodieck (1967) receptive field model for an on-center cell. Activity of bipolars can be either increased by receptor activation or decreased by amacrine cells acting as inhibitory interneurons. Bipolars are excitatory and amacrine cells inhibitory to ganglion cells. The opposite is true for off-center cells (reproduced from Johnson, Hatton and Goy, 1969).

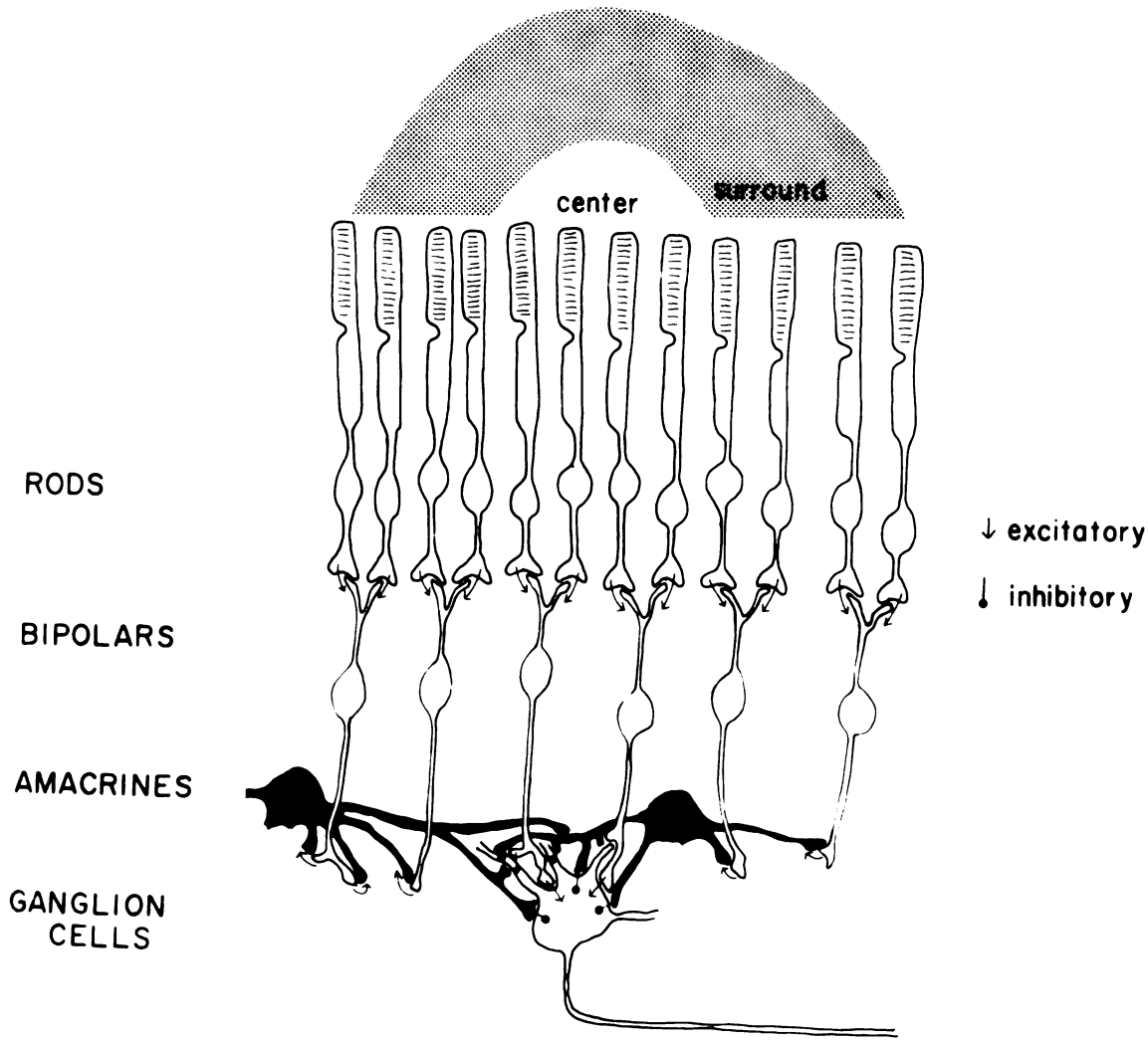
center
surround
RODS
BIPOLARS
AMACRINES
GANGLION CELLS
↓ excitatory
inhibitory

Figure 15

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BIBLIOGRAPHY

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APPENDIXES

APPENDIX A

TRACINGS OF THE ELECTRODE TRACKS

As a rule the plane of the electrode track was found to be very different from the plane of the brain section. Thus the tracks had to be traced through a large number of sections in order to determine their starting and finishing points. The sections shown in Figures A1 and A2 are the ones in which the lesions were found. Figure A3 shows a photomicrograph of the section where the lesion was found for experiment 68337. In general, recordings were only made from one puncture per experiment. One of the nine brains was lost.

Abbreviations used in the figures are taken from A. L. Berman, The Brain Stem of the Cat; A Cytoarchitectonic Atlas with Stereotaxic Coordinates. University of Wisconsin Press, Madison 1968 and are as follows:

AF - Ammon's formation
F - fornix
IC - inferior colliculus
LGD - dorsal lateral geniculate nucleus
LP - lateral complex of the thalamus
PUL - pulvinar
SC - superior colliculus
OT - optic tract
VB - ventral basal complex of the thalamus

Figure A1.--Electrode track tracings for parasagittal sections from experiments 68339, 67328, 68344, and 68320. Section shown in each case is the one in which the lesion was found. Dotted lines represent electrode tracks and the stars indicate lesion sites.

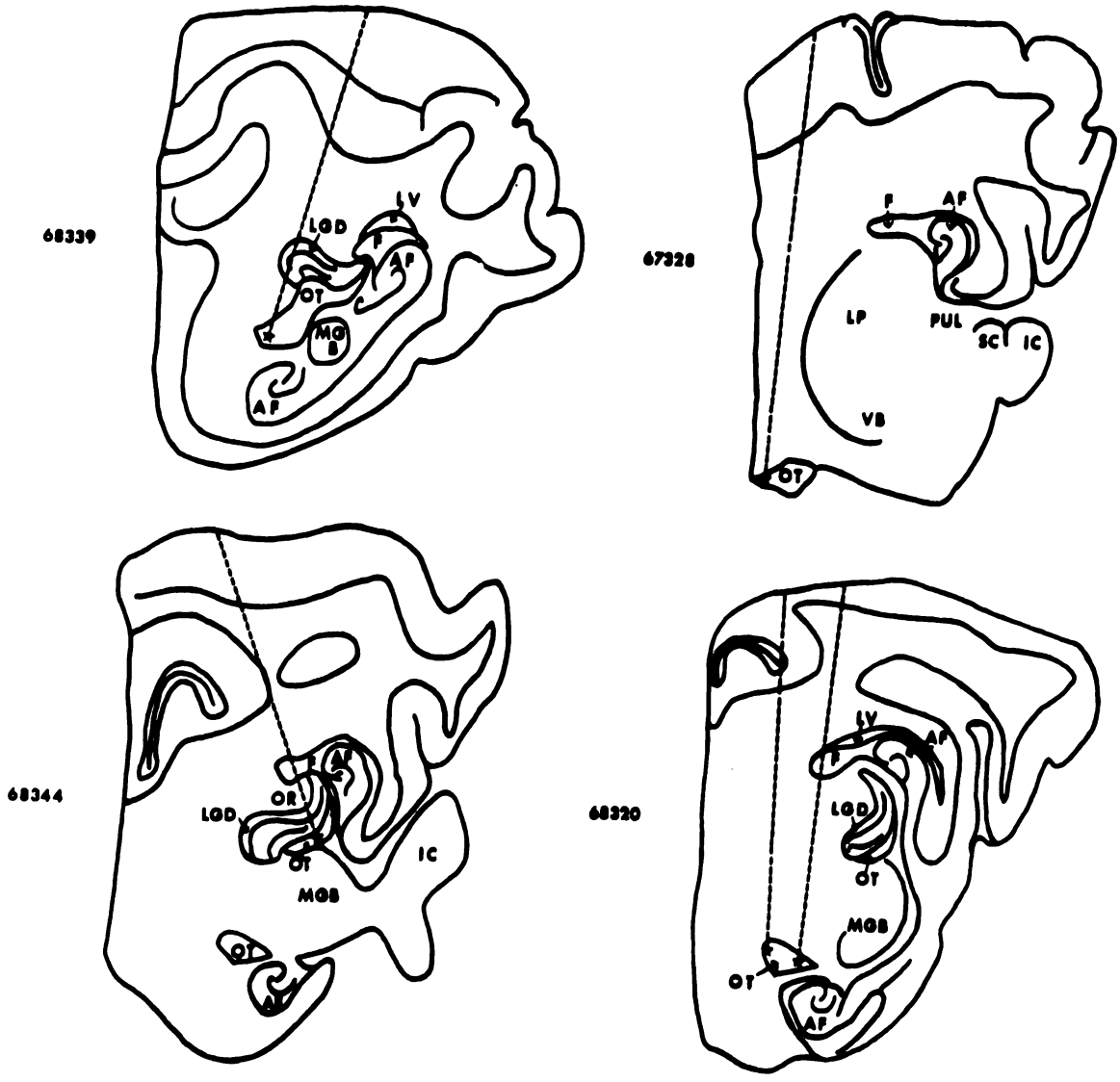

68339
LV
LGD
P
AP
OT
MGB
AP
67328
P
AP
LP
PUL
SC
IC
VB
OT
68344
P
AP
LGD
OR
OT
IC
MGB
OT
68320
LV
P
AP
LGD
OT
MGB
OT
AP

Figure A1

Figure A2.--Electrode track tracings for parasagittal sections from experiments 68346, 68400, 68401, and 68337. Section shown in each case is the one in which the lesion was found. Dotted lines represent electrode tracks and the stars indicate lesion sites.

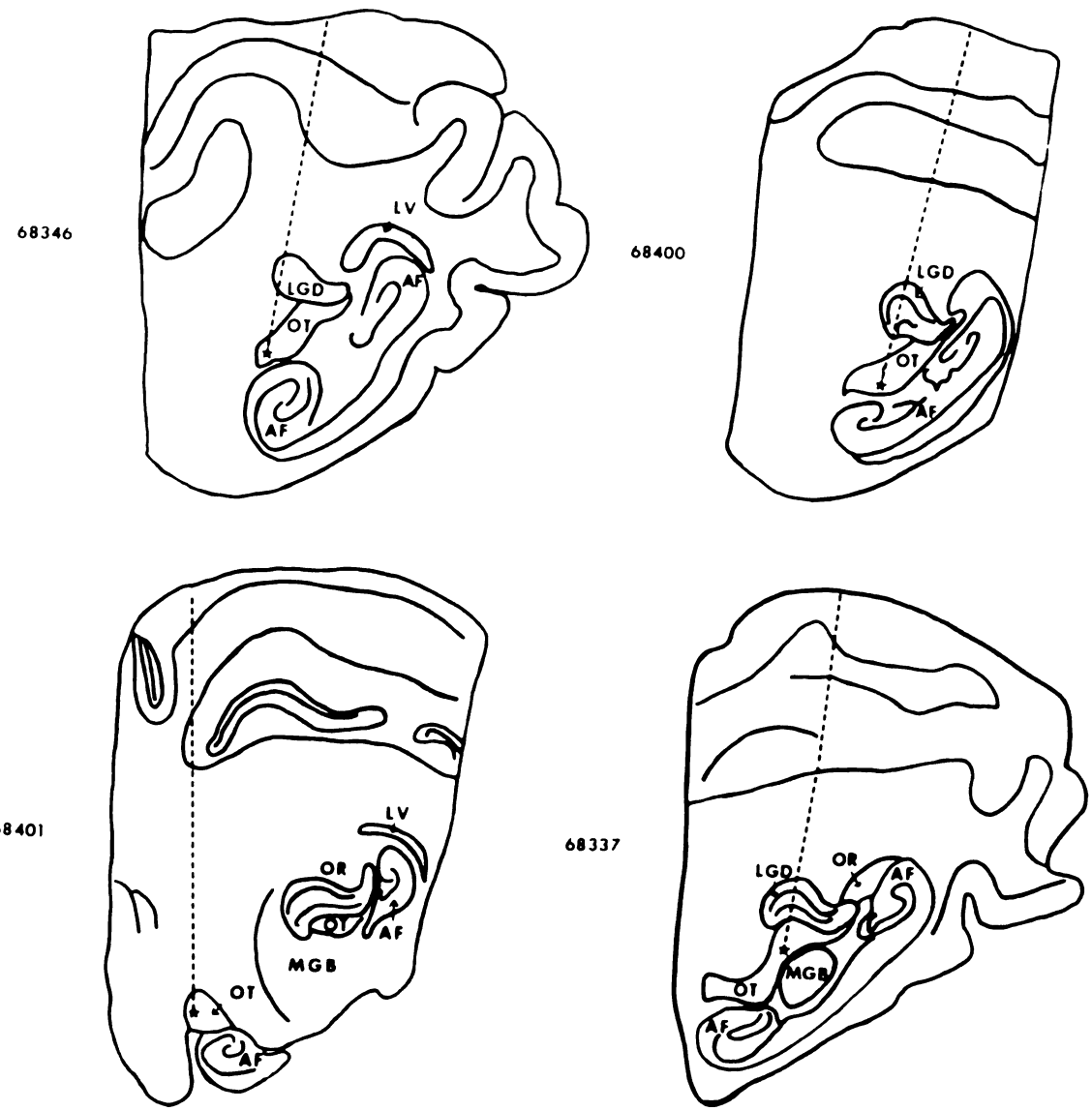

68346
LV
LGD
AF
OT
AF
68400
LGD
OT
AF
68401
LV
OR
OT
AF
MGB
OT
AF
68337
LGD
OR
AF
MGB
OT
AF

Figure A2

Figure A3.--Photomicrograph of the section, in which the lesion was found for experiment 68337.

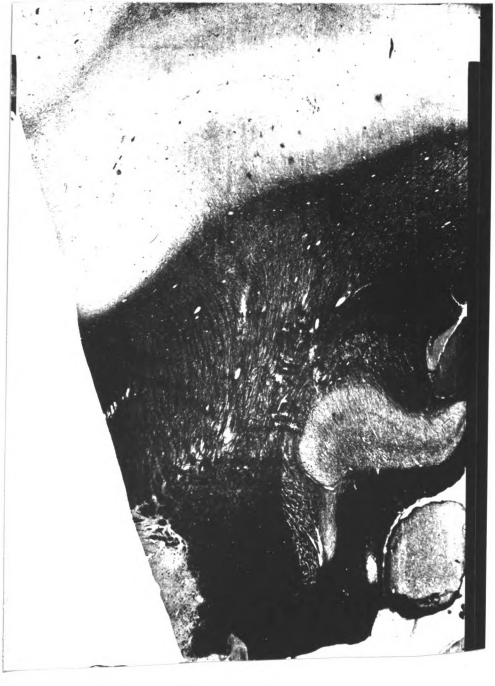


Figure A3

APPENDIX B

EXPANDED VERSION OF THE METHOD SECTION

METHOD

Subjects

Single unit recordings were made from 81 (44 on-center cells and 37 off-center cells) optic tract fibers in nine normal, adult cats.

Apparatus

The cats faced a diffusely lit, (either 0 or 1 log candle/m^2) 1-1/2 meter, translucent tangent screen (Pola Coat). The photic source, a modified 750 watt slide projector, was placed 130 cm behind the screen. The size of luminous spots presented on the screen was controlled by placing metal slides in the projector. A metal neutral density filter holder and a variable speed mechanical shutter (Wollensak Pi alphax) were attached to the movable lens of the projector. (See Figure B1.)

Recording System

Glass insulated tungsten microelectrodes were used in a conventional capacitance coupled system (See Figure B2). After being amplified by a Tektronix 122 preamplifier the biological signal was visually displayed on the upper beam of a Tektronix 502 A oscilloscope and

Figure B1.--Photograph of the photic source. Intensity was controlled by placing neutral density filters in the holder (with 2 slots) attached to the movable lens of the slide projector. The metal slides provided a means of controlling spot size. The alligator clips attached to the shutter are connected to two poles of a microswitch. The wires leading from the battery and the shutter go to the Tektronix 162 waveform generator.

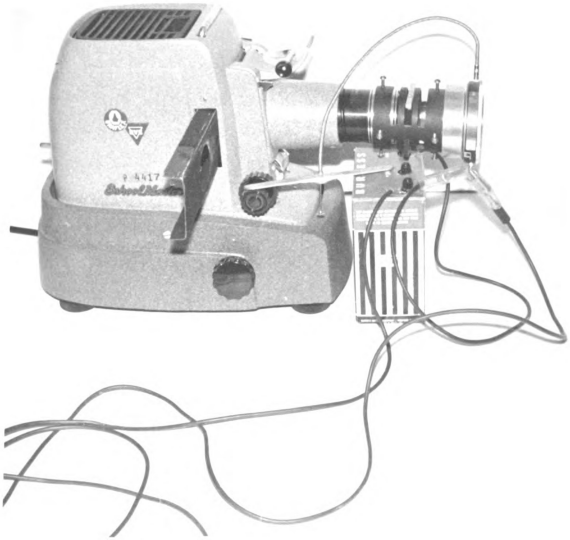
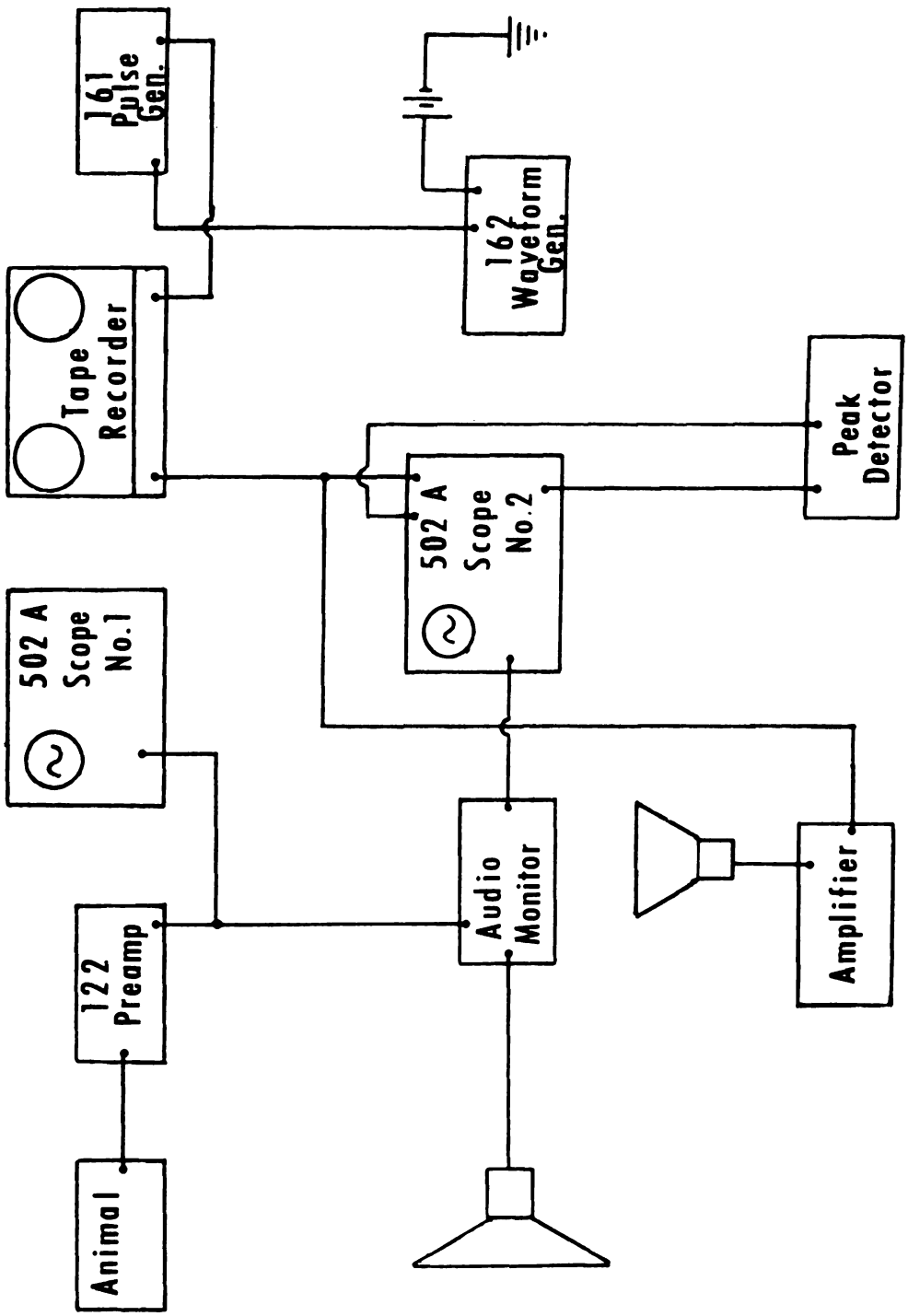


Figure B1

Figure B2.--Block diagram of the recording system. The audio monitor and 502 A Scope No. 1 were used for monitoring the unmodified signal from the brain. The 502 A Scope No. 2 was used to compare the output of the peak detector with the low frequency output of the audio monitor. This insured that pulses going to channel 1 of the tape recorder and to the second audio amplifier represented the activity of the cell being studied. The 162 waveform generator triggered the 161 pulse generator at stimulus onset. The pulse from the 161 pulse generator was recorded on channel 2 of the tape recorder.



Recording System
Figure B2

passed to an audio monitor. The low frequency filter output of the audio monitor was connected to the upper beam of a second 502 A oscilloscope. After the biological signal was amplified here it was fed to Technical Instrument Corp. Model 607 peak detector. This instrument, which served as a Schmitt trigger, permitted the experimenter to isolate the spikes of a single unit from activity of lower amplitude. The three volt peak detector output was amplified through the lower channel of an oscilloscope (which was used as a visual monitor), whose output was connected to a second audio amplifier and to one channel of a tape recorder (Magnecord 1028). The signal heard on the loudspeaker connected to the second audio amplifier was used for mapping receptive fields.

The onset of the stimulus was marked on a second channel of the tape by utilizing a microswitch which is present in the Wollensak Pi alphax shutter. When the shutter opened it closed the microswitch which was linked in a 45 volt battery circuit. The output of this circuit was used to trigger a Tektronix 162 waveform generator. Its sawtooth wave output, in turn, activated a Tektronix 161 pulse generator. The pulse from the 161 generator was recorded on the second channel of the tape.

Procedure

Initially an intraperitoneal injection of atropine sulfate (.5 mg/kg.) was given to minimize secretions.

Fifteen minutes later the animal was lightly etherized to facilitate cannulation of the femoral vein. The venous cannulation served two purposes: (1) It was used during surgery for injection of Pento Short--a short acting barbituate (.67cc/kg); (2) In a later state it served as a route for continuous infusion of a muscle relaxant, Flaxedil (gallamine triethiodide).

Following the cannulation, a bilateral cervical sympathectomy and tracheotomy were performed. The sympathectomy was done in order to decrease eye movements during the experiment (Rodieck et al., 1967). A "Y" shaped glass tube was inserted in the trachea to permit artificial respiration.

The procedure for mounting the animal's head in a head holder was at variance with the standard one. Instead of inserting metal pins in the ears, bars were attached to the zygomatic arches with dental cement. Once the head was secured, a craniotomy was performed, the dura mater was removed from the exposed area, and Inogar II (2.5 grams to 50 ml of physiological saline) was placed over the opening (See Figure B3).

Upon completion of the surgery the animal was electrically decerebrated by a technique similar to the one described by Martin and Branch (1958). Using the tentorium bone as a landmark, an electrode with a 1 mm uninsulated tip was advanced to the midbrain reticular

Figure B3.--Photograph of cat in head holder. The horizontal pins of the head holder are cemented to the zygomatic arches. The substance below the cat'e nose is dental cement which was used to prevent vertical movement of the head. The wire leading from the back of the neck is connected to earth ground through the Tektronix 122 preamplifier. The tubing in the lower right of the picture is attached to a "Y" shaped, glass tracheal cannula and to a respirator pump (not shown in the picture).

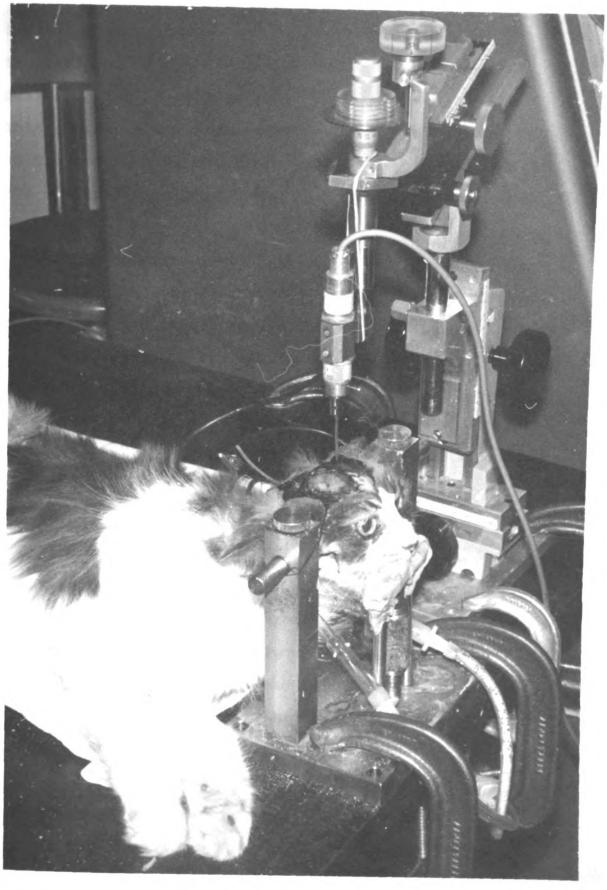


Figure B3

formation at a medial-lateral position about 2 mm from the midline. A cathodal current of 500 milliamps was delivered for 20 seconds to effect the decerebration. This procedure was repeated for a position 1 mm lateral to the initial lesion. Two lesions were also placed in the same relative position on the opposite side of the midline.

In order to immobilize the eyes an intravenous injection of 80 mg. of Flaxedil was given. A mixture of this drug (28 mg/hour) and physiological saline (6 cc/ hour) was continuously infused through the femoral vein for the duration of the experiment. Respiration was maintained by a Harvard Apparatus respirator pump (stroke volume 45 cc; respiration rate 20/min.). Body temperature was held at 38° C by a heating blanket connected to a 12 volt D.C. circuit.

Corneal contact lenses ranging from 37 to 42.25 diopters, were fitted to prevent corneal clouding. A 10 per cent solution of neosynephrine was used to keep the pupils dilated. Retinoscopy was performed in the usual manner with spherical and cylindrical lenses appropriately placed in front of the eyes to correct refractive errors.

Upon completion of the preliminaries an electrode was advanced to the optic tract. The procedure for ascertaining its location was relatively straightforward.

First, the location of the lateral geniculate nucleus (LGN) was determined. Then, using it as a landmark, the optic tract could usually be found by advancing the electrode about 5 to 8 mm below the ventral surface of its anterior portion. In terms of evoked activity the optic tract could be distinguished from the LGN in two ways: (1) Its overall response (as heard over the audio monitor) to a moving flag is one of a soft "S" sound, rather than the harsh swish found in LGN (Bishop et al. 1962a); (2) single optic tract fibers give stronger responses to diffuse illumination than lateral geniculate cells (Hubel and Wiesel 1961).

Once the tract was located the electrode was allowed to remain stationary for 15 minutes. Then it was advanced in small increments until a fiber could be isolated. The fiber's receptive field was mapped from the rear of the tangent screen with .2° dim, luminous spots presented on pieces of tracing paper taped to the screen. The papers were kept as permanent records of the receptive fields.

Threshold Experiments.--Thresholds for various sized spots--placed in the most sensitive portion of the receptive field--were determined by varying their intensity in .1 log unit steps while listening to changes in activity over the loudspeaker, i.e., the signal which had been filtered for low frequencies and fed through

the Schmitt trigger circuit. For 8 of the 21 cells studied, thresholds were also determined by analyzing changes in maintained (spontaneous) firing with a computer of average transients (C.A.T.). The threshold values from the two techniques were never more than .1 log unit apart.

Suprathreshold Experiments.--The luminance of various spots, ranging from .1° to 7°, was varied in .3 log unit increments over a 4.2 log unit range. Because most diffusing surfaces are directional, luminance values have been expressed in threshold units, i.e., log units above threshold intensity; or in terms of neutral density filter values (where smaller numbers represent greater luminance levels). The duration of stimulus pulses was 920 msec.; their rise time was 5 msec. Each stimulus was repeated 15 times at a rate of .2 cycles/second and always presented in the most sensitive portion of the receptive field. Upon completion of recording from a unit its receptive field location, with respect to the area centralis, was ascertained by the reversible ophthalmoscopic technique (Bishop et al. 1962b). In this technique (See Figure B4) the rectangular beam of an opthalmoscope is fixed on the edge of the optic disc while viewing the fundus. The ophtahlmoscope is then revolved 180° and the rectangular beam is traced onto the tangent screen. This procedure is repeated for several points tangent to the optic disk until a suitable map is obtained.

Figure B4.--Schematic showing the reversible ophthalmoscopic technique. The fundus (C) was viewed by the experimenter through an ophthalmoscope (B). The slit from the ophthalmoscope was maneuvered until it was tangent to the optic disc (D). The opthalmoscope was then rotated 180° and the slit was traced onto the 1-1/2 meter tangent screen. This procedure was repeated until the projected optic disc was adequately mapped.

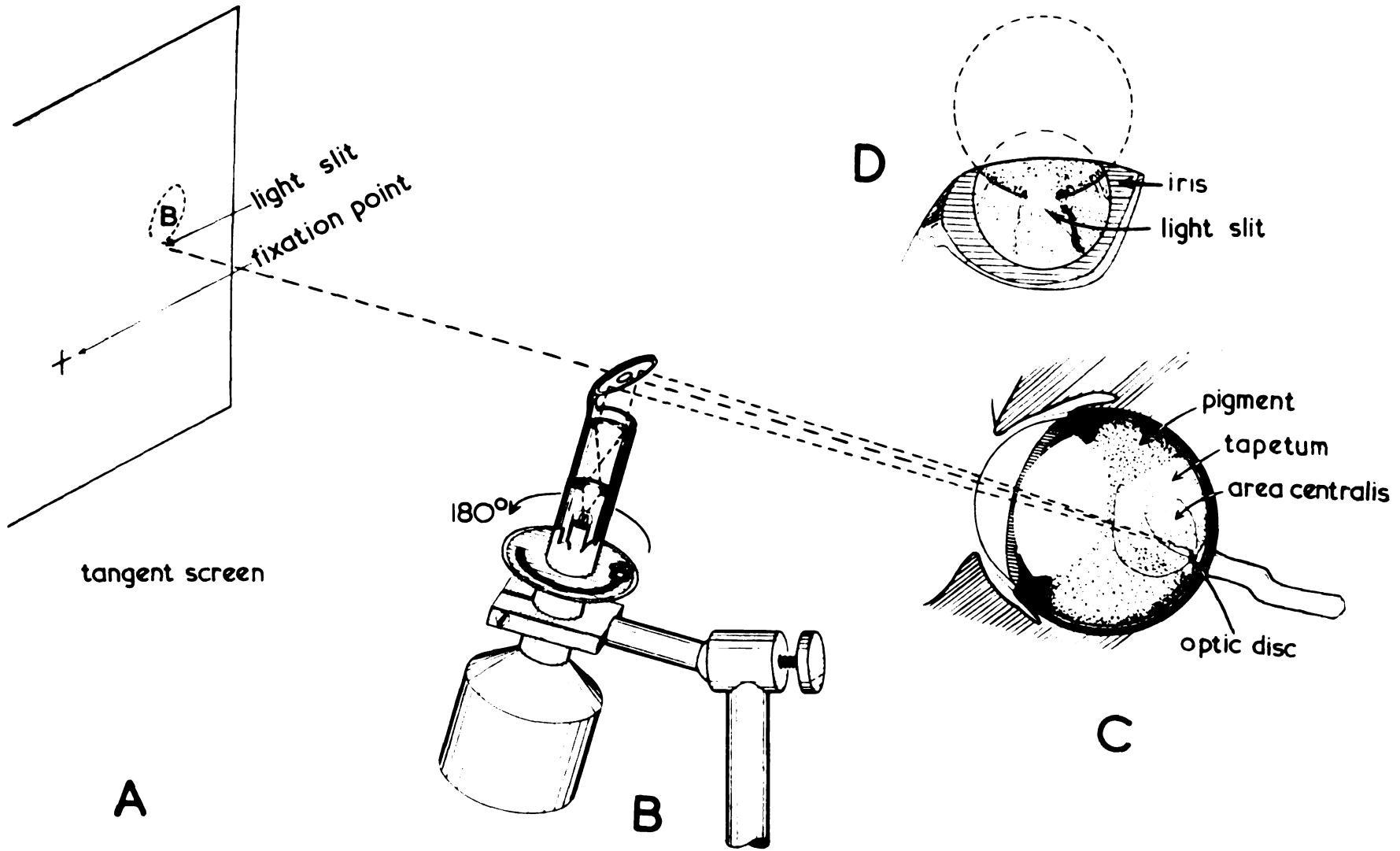

B
light slit
fixation point
tangent screen
A
180°
B
D
iris
light slit
pigment
tapetum
area centralis
optic disc
C

Figure B4

The position of the receptive field relative to the disc is then measured. This measurement can be converted to one where the area centralis is the reference point by presuming that, on the average, the area centralis is located 13.6° temporal and 5.5° superior to the optic disc (Vakkur et al. 1963).

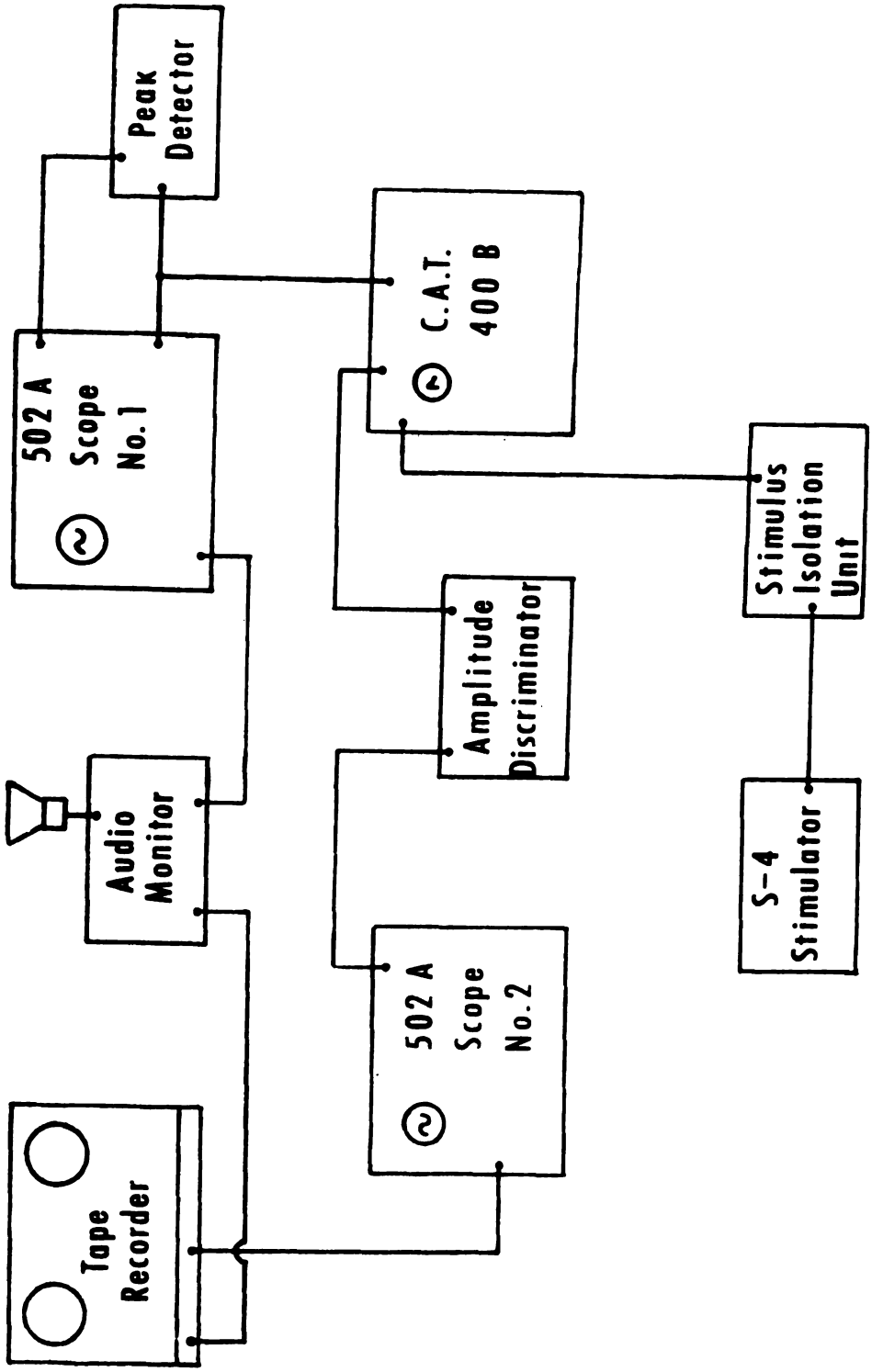
Typically data from 5 to 15 fibers were collected in a single puncture. After completing work in a puncture, a microlesion was usually placed at the recording site.

When the experiment was terminated the cat was intracardially perfused with .9 per cent saline, followed by a mixture of 10 per cent formalin and .9 percent saline. The brains were embeeded in celloidin and sectioned parasagitally. Alternate sections were stained with thionin for cell bodies and hematoxylin (Weil or Heidenhain method) for myelinated fibers. Recording locations were confirmed by tracing electrode tracks and looking for the microlesions which had been placed at the recording site during the experiment.

Data Analysis

The system for analyzing data included the aparatus shown diagrammatically in Figure B5. There were two major components of the system: one that was concerned with processing the neural activity which was recorded

Figure B5.--Block diagram of data analysis system. The audio monitor, 502 A Scope No. 1 and the peak detector were concerned with processing the data from channel 1 of the tape recorder. The loop between the peak detector and the 502 A Scope No. 1 provided a means of monitoring the input to the C.A.T. The amplitude discriminator and 502 A Scope No. 2 were concerned with the processing of the stimulus marker, i.e., the pulse that corresponded to the stimulus onset, recorded on channel 2 of the tape recorder. This signal was used to trigger the analysis sweep of the C.A.T. The S-4 stimulator was used to control its sweep speed.



Data Analysis System
Figure B5

on channel 1 of the tape recorder and one that dealt with processing the time marker signal that was recorded on channel 2.

The spike activity from channel 1 was led through an audio monitor before being visually displayed on a 502 A oscilloscope. The vertical output of the oscilloscope was connected to a peak detector which in turn fed square wave signals to both the C.A.T. 400 B, where they served as the data for generating average response histograms, and back to the oscilloscope. The loop between the oscilloscope and the peak detector enabled the experimenter to monitor the input to the C.A.T.

After being amplified by a second oscilloscope the signal from channel 2 was fed to an amplitude discriminator. (In this context the amplitude discriminator is functionally equivalent to the peak detector.) The amplitude discriminator's output was connected to the C.A.T., in order to trigger its analysis sweep. The analysis time (bin width size), which was usually 5 msec., was controlled by an S-4 stimulator.

After being analyzed by the C.A.T. the data were usually printed out on a teletype. The blocks of printed numbers, which represented the sum (over 15 stimulus cycles) of spikes during 5 msec. time intervals, were used as the basis for quantifying the magnitude of the transient and steady state responses.

Average response histograms could be visually displayed and photographed by connecting the "Y" axis output of the C.A.T. to the vertical amplifier of an oscilloscope.