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Reprinted from EXPERIMENTAL NEUROLOGY
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Volume 15, Number 3, July 1966
Printed in U. S. A.

EXPERIMENTAL NEUROLOGY 15, 363-376 (1966)

Retinal Receptive Field Changes Produced by Auditory and Somatic Stimulation

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Received February 10, 1966

The existence of efferent influences on the cat retinal ganglion cell was shown in previous studies. Those experiments, utilizing both chronic macroelectrode and acute microelectrode techniques, demonstrated responses in the optic nerve to auditory and somatic stimuli. Afferent activity in the optic nerve was also found to be modified by these stimuli. The present experiments were undertaken as an extension of this effort. Retinal receptive fields were mapped in immobilized cats. The value of the mapping technique used for these experiments is that it provides an accurate definition of receptive field boundaries. Auditory or somatic stimuli were shown to induce reliable dimensional changes in 76% of the receptive fields examined. Changes in the firing strength of units were also produced by the nonvisual stimuli. These changes were not directly correlated with the dimensional changes observed. No lawful relationship was found between direction of change and the type of efferent stimulation or type of receptive field or both. Changes in receptive field dimension were also elicited by a change in ambient illumination. An interaction between the changes caused by nonvisual sensory stimulation and those brought about by a change in ambient illumination was found in two instances.

Introduction

In earlier studies we demonstrated efferent influences on the retina (12, 13). These showed that the firing patterns of optic nerve fibers could be altered by auditory and somatic stimuli. It seemed reasonable, therefore, to ask what the functional significance of such efferent control might be. Alterations occurring in the receptive field under such conditions would provide some initial answers to this question.

Hartline (5, 6) defined the receptive field of an optic nerve fiber as "that region of the retina which must be illuminated to obtain a response in any given fiber."

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[1] This research was supported by USPHS Grant MH 03732 and Department of the Army Contract DA-49-193-MD2328.

Kuffler (8) found that there were two types of responses in cats: those evoked when the stimulating light fell on the central, and those evoked when it fell on the peripheral zone of the receptive field. He thus divided receptive fields into two categories, on-center and off-center, according to which response was elicited by stimulation of the center. However, the extent and character of a receptive field is not fixed but is dependent on a variety of factors (2, 5, 7, 10). For instance, the size and intensity (5, 7) of the exploring spot of light alter the receptive field as does the state of adaptation of the eye: Barlow, Fitzhugh and Kuffler (2) have shown in the cat that dark adaptation abolishes the surround response of the field and increases the central diameter.

Intensity of illumination and the state of adaptation are also known to affect the response pattern of optic nerve fibers to a flash (4). We were thus led to the hypothesis that whenever the response pattern of a fiber is altered by adaptation, efferent activity, or any other factor, concurrent changes in the receptive field of that same fiber should also be present. Arden's (1) findings in the lateral geniculate body provide some support for this hypothesis. He showed that repetition of a visual stimulus causes progressive changes both in the resting activity of the cell and the size of its receptive field.

Efferent pathways to the retina have been demonstrated (9, 12, 13). Our previous study (13) showed that activation of these pathways by means of auditory and somatic stimuli can modify the firing pattern of retinal ganglion cells. In the present investigation the effects of auditory and somatic stimulation on the visual receptive fields of single optic nerve fibers were investigated. These stimuli were found capable of producing reliable changes in the organization of visual receptive fields.

Methods

Twelve adult cats were used in this study. The method and procedure used were described in the previous paper (13).

Results

Types of Receptive Felds. A total of 140 optic nerve fibers were recorded. Forty-four of these were studied in sufficient detail to allow classification of their receptive field organization. Twenty of those classified were on-center and twenty-four were off-center fields. The diameter of the center of the fields ranges from 0.6 to 25°.

A receptive field was first mapped by a moving spot of light, and then remapped during presentation of either the binaural auditory stimulus or the shock; the field was then remapped with no auditory or somatic stimulus to determine if any "drift" or change had occurred irrespective of the stimulus presentation. Twenty-four fields were studied during the separate presentation of both stimuli. Of the forty-four fields plotted, thirty-one showed a return to normal, i.e., the first and third mappings were similar. The remaining fields were too labile to allow any firm conclusions about the changes observed (Discussion).

Changes in Receptive Field Organization with Auditory Stimulation. Auditory stimulation was used as a "conditioning" stimulus in the analysis of thirty receptive fields. Of these, 80% were modified as a result of the auditory stimulus (Table 1). No consistent relationship was found between direction of change and type of receptive field. Relatively more on-center receptive fields were altered by click and off-center fields.

Figure 1A is a plot of the on-center receptive field of a unit that did not show any spontaneous firing. Because of this the inhibitory annular surround was not revealed by the method of mapping used in this study. The small diameter of the center, 1°, makes the change in width due to click appear minimal. It is, however, on the order of a 14% increase. The more obvious change is shown on the ordinate of the plot where the number of spikes is plotted. There was a 53% increase in the number of times the unit fired to the spot of light when it was paired with auditory stimulation.

Figure 1B is the same receptive field mapped with the spot of light moving in the reverse direction. The spatial dimension of the field, when mapped in this fashion, is seen to be much larger than when mapped with the stimulus moving in the opposite direction; also the effect of click on the organization of this field is less pronounced, but is in the same direction.

A relative independence between strength of firing and spatial dimension of visual receptive fields was observed. In an attempt to increase background firing to show the inhibitory surround of this field, ambient light was increased by 0.25 ft-c. This did not have the desired effect but it did increase the spatial dimensions of the field by 29% whereas the strength of firing was increased by only 14%.

The responses of this optic nerve fiber to *diffuse* flash were also studied. There was then no discernible change in the firing pattern when the click was paired with the flash.

Figure 2A is the map of an on-center field in which the effect of audi-

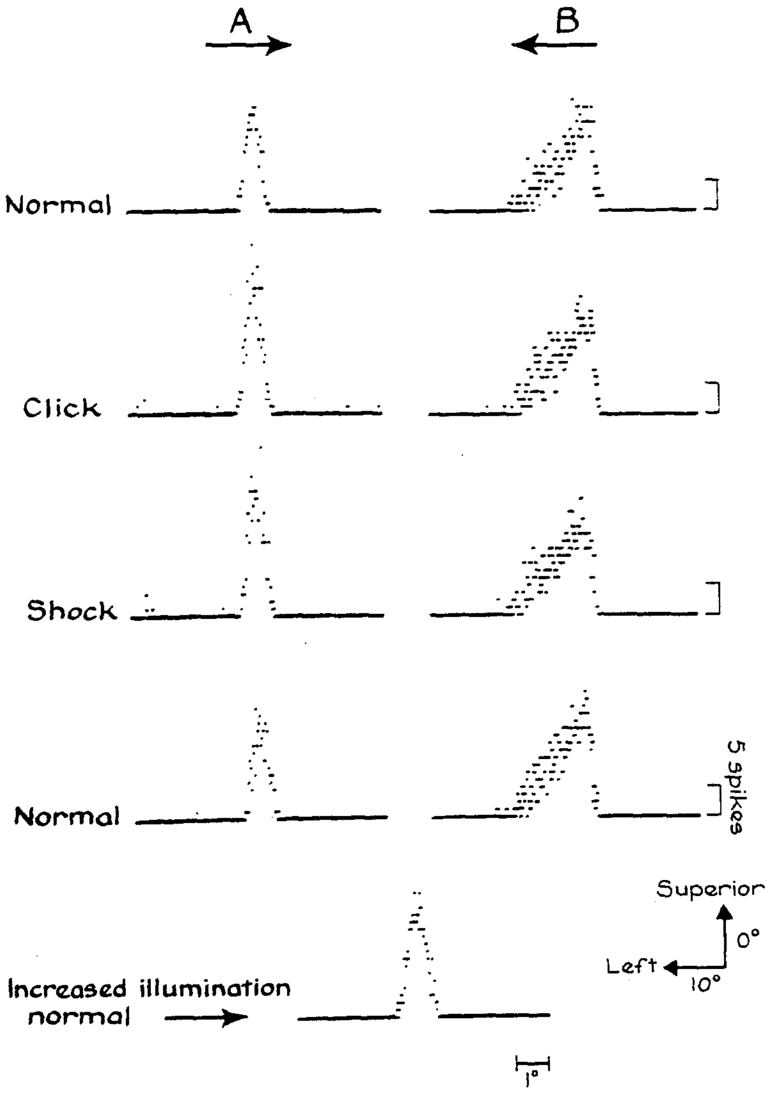

FIG. 1. On-center receptive field mapped in horizontal plane. A. The luminous disc is moving from right to left. The response histogram in the first row was plotted under "normal" conditions and is used as a baseline. This field was then replotted during click presentation. The click caused an increase in dimension of the field of 14%, whereas the strength of firing characteristic was increased 53%. Shock

tory stimulation on strength of firing and field dimension are in opposite directions. This unit, as the previous one, did not have spontaneous activity. Click increased the field center diameter by 12%, whereas it decreases the strength of firing by 9%.

Figure 2B is the same field mapped with the stimulus moving in a vertical plane. This plot is similar to that of Fig. 2A where the motion was in the horizontal plane. The effect of click in both cases was similar.

The off-center field of Fig. 3 is much larger than the previous two fields. (There was a tendency in the group of receptive fields studied for the off-center fields to be larger than the on-center and for the larger receptive fields to be located more peripheral than the smaller ones.) This field dimension was decreased by 17% as a result of the auditory stimulation.

The type of changes produced by auditory stimulation in four receptive fields proved difficult to quantify. This type of alteration consisted of a decrease in the sharpness of the boundary separating the antagonistic annular zones of the field. The on-center field of Fig. 4 is an example of such a change.

Receptive fields with variable baseline dimensions were sometimes encountered (Table 1). This type of field was excluded from statistical consideration. However, in certain instances the presence of variability did not exclude the possibility of demonstrating efferent induced changes. This was possible when the amount of variability was small or when the auditory evoked change was great or both. Figure 5 is the map of a receptive field in which both these conditions were met.

Changes in Receptive Field Organization with Shock. Twenty-five receptive fields were mapped during shock presentation. All but one of these were also mapped during auditory stimulation. In two of these

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presentation caused a similar change in the strength of firing but only a 7% increase in spatial dimension. The fourth row in A is a control plot of this field. The dimensions are seen to be similar to the first normal response histogram. B. The same field mapped from right to left. The contours and dimensions of the field are different from A. The central diameter is twice as large. Click and shock cause a 12% ± 6% increase in field size, respectively. The strength of firing characteristic was too variable to permit a comparison. The last row is a response histogram of this field mapped as in A but with an increase in ambient illumination of 0.25 ft-c. The spatial dimension is increased by 29% and the strength of firing was increased by 14%. Speed of luminous disc: 1.87°/sec. Disc size: 0.3°. Number of averages: 5. Lower right corner indicates position of receptive field in visual field.

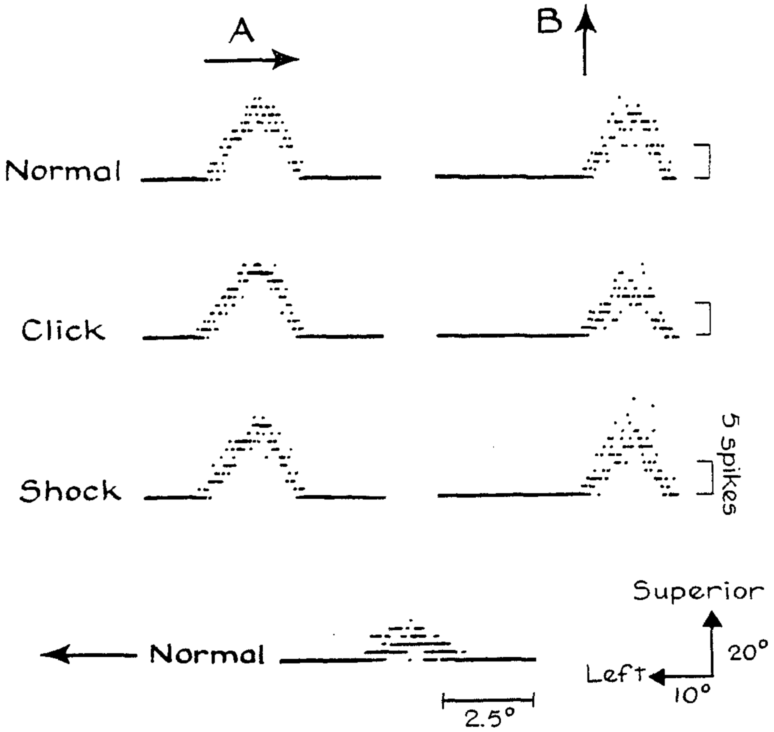

FIG. 2. On-center receptive field with small, but measurable and reliable changes induced by click and shock presentation. A is mapped with the disc moving from left to right. Click induces a 12% increase in central diameter and a 9% increase in diameter but does not affect strength of firing. B is mapped with disc moving upward in vertical plane. The contour of this response histogram is similar to A but the central diameter of the field is slightly less than A. Click induces a 10% increase in central diameter and an 11% decrease in strength of firing, whereas shock causes a 7% decrease in diameter, and a 17% increase in strength of firing. The bottom row is a response histogram of the field with the disc moving in the reverse direction of A. A marked difference is seen in both the contour and diameter of the field. Speed of disc: 1.87°/sec. Disc size: 0.3°. Number of averages: three.

twenty-four fields the changes caused by the shock were in the opposite direction from those induced by the click (Table 1).

The shock-elicited change in the spatial dimension of the receptive field of Fig. 1A was less than that induced by the auditory stimulus. However, the change induced in the strength of firing characteristic by the two stimuli was similar. This again illustrates the relative independence of these two characteristics.

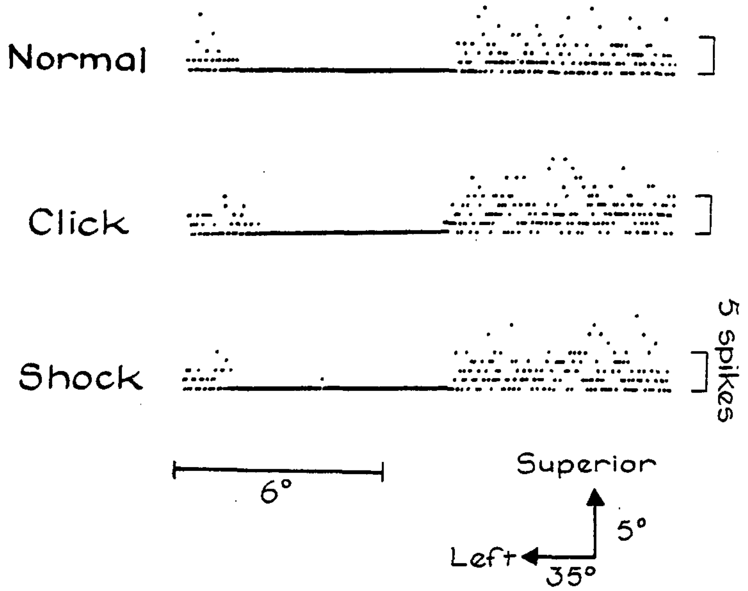

FIG. 3. Off-center field mapped with disc moving from left to right. Click causes a 17% reduction in central diameter. Shock has no effect on the central diameter. Speed of disc: 15°/sec. Disc size: 0.6°. Number of averages: eight.

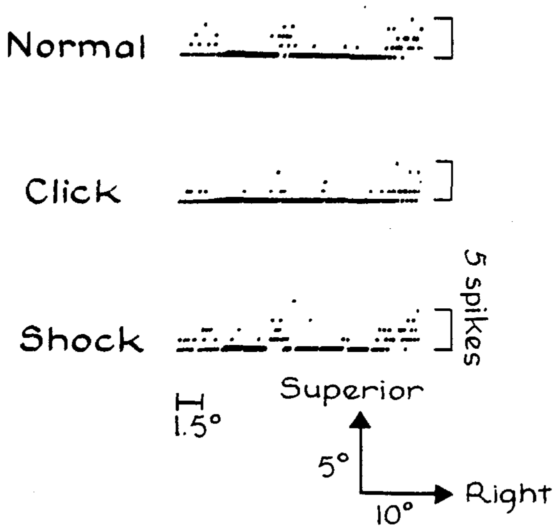

FIG. 4. On-center receptive field mapped with disc moving from left to right. Obvious changes are induced in this field by both click and shock. However, the character of this change does not permit quantification. Speed of disc: 3.75°/sec. Disc size: 0.6°. Number of averages: three.

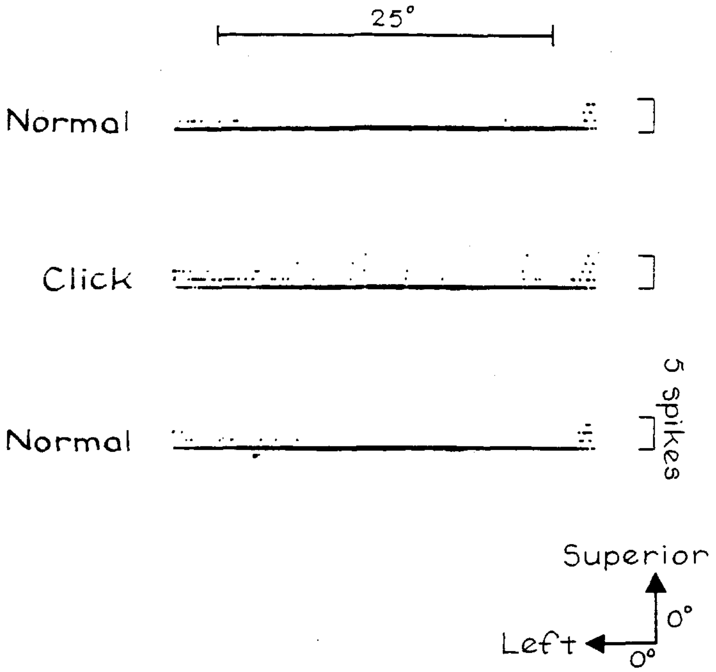

FIG. 5. Response histogram of an off-center receptive field with slight variability in boundaries. The changes induced by click, however, are great enough to be seen in spite of this variability. Speed of disc: 3.75°/sec. Disc size: 1°. Number of averages: three.

The two nonvisual stimuli produced opposite changes in some receptive fields, Fig. 2B. In this case, both the strength of firing and spatial dimension were oppositely affected by the two stimuli. This differential effect was found only when the receptive field was mapped with the spot of light moving in the vertical plane. Figure 2A is a plot of the same receptive field with the spot of light moving in a horizontal plane. With this type of movement, the effect of shock, though smaller, was in the same direction as that of the click.

Table 1 is a summary of these results. Several trends can be observed in this table. The two conditioning stimuli, for example, caused a greater number of increments rather than decrements in field size. It is, however, difficult to say of what significance this may be.

Effects of Ambient Illumination. Four fields, three off-center and one

TABLE 1
FORTY-FOUR RECEPTIVE FIELDS[a]

	On-center			Off-center			Total				
	Inc.	Dec.	NC	Inc.	Dec.	NC	Inc.	Dec.	NC	% Change	Drift
Click											
No. of units	7	4	1	7	6	5	14	10	6	80	12
Range of change (%)	5-23	9-30		3-40	8-38						
% of units	58.3	33.3	8.3	38.9	33.3	27.8	46.7	33.3	20		
Shock											
No. of units	5	4	3	6	3	4	11	7	7	72	13
Range of change (%)	5-15	5-9		6-39	12-38						
% of units	41.7	33.3	25	46.2	24	30.8	44	28	28		
Total	12	8	4	13	9	9	25	17	13	76.4	25
%	50	33.3	16.7	42	29	29	45.5	30.9	23.6		

[a] Changes refer to spatial dimension only. Twenty-four fields were mapped with both click and shock. In two of these the changes to click and shock were in opposite directions. Changes in four of these were of the same magnitude. In twelve, click produced changes that were greater than those caused by shock and in eight the converse was true. Abbreviations: Inc. = increase; Dec. = decrease; NC = no change.

on-center, were remapped with an increase in ambient illumination of 0.25 ft-c. The central diameter of the off-center fields was decreased by the illumination. The on-center field (Fig. 1) was increased by the increase in light. The effect of click and shock on two of these fields, with the increased illumination condition, was the reverse of its initial effect under the normal testing illumination. The off-center of the receptive field in Fig. 6 was decreased 31% by the increase in illumination. The original effect of shock and click was to increase the center diameter slightly. Upon an increase in ambient illumination, the effect of the two stimuli was to cause a decrease in the center size.

Discussion

Characteristics of the Receptive Fields Studied. The almost equal division of the two types of fields is in agreement with the literature (14). The range of center sizes, however, is larger than that reported by Wiesel (14). This discrepancy is likely due to the fact that Wiesel's sample was restricted to the area centralis and that we were unable to differentiate the transitional on-off zone from the center of the receptive field with the moving-light technique employed in this study. This zone probably adds to the central diameter in many cases, especially in on-center fields.

The occurrence of "drift" in this study deserves mention. Though most of the fields examined were stable, approximately 30% displayed "drift." Possible explanations for this include a long-lasting effect of the auditory or somatic stimuli, or a phenomenon similar to that found by Arden (1) in the lateral geniculate body; i.e., repetition of a visual stimulus causes progressive changes in receptive field organization.

In general the characteristics of the receptive fields studied were in close agreement with receptive field characteristics as described by Rodieck and Stone (11). There were, however, a few exceptions: Some receptive fields (Fig. 1A an B; and Ref. 13), produced a different histogram when scanned in opposite directions. As the scanning was done on the same axis it would seem difficult to attribute these differences to a spatial asymmetry of the receptive field. Also absence of component "a" was found to be more the rule than the exception.[2] Moreover, some units were found to be responsive to the absolute level of illumination (13).

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[2] Component "a" in Rodieck and Stone nomenclature is the change in activity that is produced when the leading edge of the image crosses the surround of the receptive field.

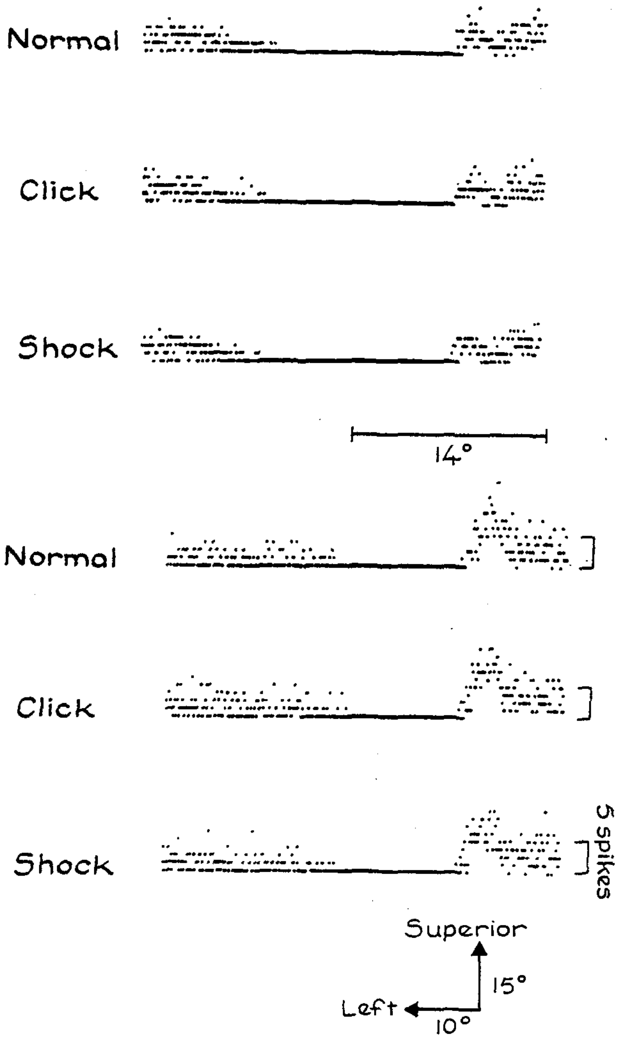

FIG. 6. Off-center receptive field mapped with disc moving from left to right; upper three: 0.05 ft-c; lower three: 0.3 ft-c. With an increase in ambient illumination of 0.25 ft-c the central diameter of the normal field is decreased 31%. With the 0.05-ft-c illumination, click and shock cause a 3.7% and 5% *increase,* respectively, in the central diameter. With increased illumination, click and shock cause an 11% and 4% *decrease* in central diameter, respectively. Speed of disc: 3.75°/sec. Disc size: 0.9°. Number of averages: four.

Scanning Speed. The response of any given unit to the moving disc was found to be dependent upon the speed of scanning; in general, the type of response was correlated with speed in a regular fashion as described by Rodieck and Stone (11).

Effect of Increased Ambient Illumination. Kuffler (7) found a decrease in receptive field size with increased illumination irrespective of type of field. In the present study the off-center fields were found to decrease and the one small on-center field examined increased in diameter when illumination was increased. More interesting is the reversal of effect of efferent stimulation upon increasing illumination.

Changes in Receptive Field Organization by Extravisual Stimulation. Auditory and somatic stimuli were found capable of modifying visual receptive fields. Some of the possible causes of artifact were discussed in the previous papers (12, 13). Homatropine and an artificial pupil were used in this work to avoid the possibility that pupillary changes, due to incomplete paralysis of the iris, would contaminate the results. Flaxedil and Cyclogyl were also used in sufficient dosage to insure complete paralysis of the extrinsic and intrinsic muscles of the eye. Because the level of light adaptation has been shown to affect receptive field organization (2), great care was taken to maintain a constant background level of illumination during the experiment. Moreover, each receptive field was mapped several times with and without auditory and somatic stimuli to make sure that both the normal and the modified condition could be reliably reproduced.

The hypothesis that changes in firing pattern of an optic nerve should be accompanied by concurrent modifications in its receptive field is supported by these experiments. However, a simple relationship between firing pattern changes and receptive field changes was not found.

In the previous study (13) the firing patterns of only a small fraction of units were modified by click and shock. In this study one is impressed by the large fraction of visual receptive fields altered by these same stimuli. In the present experiments the greater sensitivity of the receptive field measure was explored further. Twelve units whose *receptive fields* were altered by click or shock were tested by means of diffuse visual stimulation. Only two of these showed clear-cut firing pattern changes when click and shock preceded the *flash.* This greater sensitivity of the receptive field is not surprising when one considers the large number of potentially modifiable cells and interconnections which determine one receptive field. On the other hand, a diffuse flash simultaneously stimulates a large surface of the retina so that the usual differential between center and surround is in effect balanced out.

The direction of change induced by the click and shock was largely unpredictable; however, most units showed expansion rather than a contraction of the field. A lack of any precise correlation is perhaps due to the absence of significance to the animal of the stimuli used.

Receptive field boundaries are not to be considered immutably fixed. Kuffler (8) had already noted the "flexibility and fluidity" of receptive fields. They are influenced by the present visual environment and the immediate past history of the retina. The results presented here strongly suggest that, in addition, visual signals are modified even at the retinal level by the activity of other sensory systems. Contrary to what has been supposed by others (2, 3), it seems reasonable to assume that the efferents to the retina serve as a programmed control system necessary if visual stimuli are to be processed meaningfully.

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