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Afferent and Efferent Activity in Single Units of the Cat's Optic Nerve

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Auditory and somatic stimuli have been shown in a previous study to elicit efferent activity in the optic nerve of cats; this activity was recorded with gross electrodes. This study was undertaken with the purpose of identifying efferent activity at the single unit level. Afferent units and the changes induced in their activity by auditory and somatic stimulation were also analyzed. Twenty healthy, adult cats were used; records were taken from 300 units. Twenty-nine of these units were found to be selectively activated by the nonvisual stimuli and classified as efferent. Among the afferent fibers, forty-eight were modified in their activity by auditory and somatic stimulation. Two types of afferent units with characteristics not previously reported for the cat's retina were indentified during the course of this work. These were units responsive to the light flux, and units responsive to the direction of movement of a spot of light.

Introduction

Efferent fibers in the vertebrate retina have been described by anatomists (2, 11, 13, 22, 24, 29, 31, 34, 36). These fibers terminate in the seventh layer of the retina around the amacrine cells and their origin was traced histologically as far back as the optic papilla. No anatomical proof that they exist in the optic nerve has been forthcoming (7, 28, 29, 36) except for Maturana's electron microscopical study of the optic nerve of the frog (22). In fact, Brindley (8, 9) has categorically claimed that there are no efferent optic nerve fibers to the cat's retina.

Yet indirect evidence for the existence of efferent control of retinal function has been provided by a number of physiological studies (1, 12, 14, 17, 18, 27), though many of these have been challenged (8, 9). More recently Spinelli, Pribram and Weingarten (33) demonstrated that centrifugal optic nerve responses could be evoked by auditory and somatic stimulation. These records were obtained from electrodes im-

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planted in intact, awake cats. The efferent nature of these respons attested by the fact that they were present in atropinized, cu preparations and disappeared when the optic tracts were cut ce to the electrodes. Further, nonvisual sensory inputs were shown to both the ERG and flash-induced optic nerve potentials.

Centrifugal control of afferent systems is of considerable theo significance (21, 26, 30). The present study was undertaken as a co tion of the effort to clarify and define the physiological significa this efferent influence on the retina. To this end, single unit acti the optic nerve was investigated in acute preparations. Single units tively responsive to auditory and somatic stimuli were identified; tionally, modifications of afferent activity to flash induced by no stimuli were studied.

Materials and Methods

Surgical Procedures. Twenty adult cats were used. All were anestl with thiopentol sodium (Pentothal 25 mg/ml of saline solution, small repeated dosages until the desired level of anesthesia was ob The necessary level of anesthesia was then maintained by the in of incremental doses until all surgical procedures were completed. pine sulfate (0.4 mg/kg, ip) was given before surgery. Meanwhile a polyethylene tube was inserted in the radial vein for administrat saline, gallamine triethiodide (Flaxedil) and glucose as required. Co paralysis essential to prevent eye movements was maintained thro the experiment. Homatropine, Dorsacaine, Phenilephrine, were i routinely in the eye (33). Contact lenses (1 positive diopter) wer to protect the eye and correct for accommodation. A tracheal c was inserted to allow artificial respiration of the cat (respirator 25/min; stroke volume: 100 ml). All incisions and pressure point heavily infiltrated with 2% xylocaine and also with a solution in procaine (Zyljectin); this second local anesthetic remains active period of several days.

An incision was made in the skin over the calvarium and th edges secured to a metal ring above so that a pool of warm min could be made later. A small trephine hole was made in the skull a dura mater opened. The exposed cortex was then covered with oil; at other times a solution of agar in saline was used to minimiz pulsation. The experiments lasted an average of 10 hours; it can sufficiently emphasized that the utmost care had to be taken experiment to avoid even the slightest discomfort to the animal (

Stimuli were presented every 2 sec and consisted of low intensity flashes of light, delivered by a Grass PS-2D photostimulator set at the minimum intensity and with the flashing bulb placed at about 1 meter; low intensity shocks in the form of rectangular pulses of 1-msec duration and of sufficient amplitude to produce a slight twitch (this intensity was set before giving Flaxedil to the animal) were applied to one of the paws; auditory stimuli were produced by passing a rectangular pulse (9v, 1 msec), through a pair of earphones (Telex HFV 91) connected to the hollow bars of the stereotaxic apparatus.

General Recording Techniques. An array of four microelectrodes was lowered stereotaxically and the tips aimed at the intracranial end of the optic foramen. The microelectrodes were made with tungsten wire tapered electrolytically in a way similar to the one described by Hubel (15), and insulated with several coatings of a vinyl polymer (Stoner Mudge S-986-015). The impedance of the electrodes used ranged from 3-10 megohms and was measured with a rectangular pulse 0.5 msec in duration. Four solid state devices (F1 100) selected for low noise were used in a source-follower configuration. (This is the equivalent of the cathode-follower in tubes.) These devices have an input leakage resistance which is typically 10^{15} ohms; their input capacitance varies from 2.5 to 3.5 pf. In a source-follower the gate-source (gs) component of the input capacitance is reduced to $C_1gs = Cgs\ (1\text{-}g)$, where g is the voltage gain; therefore, it can be easily seen that with this device used in a source-follower configuration, an input impedance of 10^9 ohms or higher can be achieved (measured at 1000 cycle/sec). The input stages were mounted directly above the microelectrodes. The cat was positioned comfortably on a heating pad and the rectal temperature maintained at 38 ± 0.5 C.

The output of the source-followers was each capacity coupled to one side of the differential input of a Tektronic 122 amplifier; the other input lead of the Tektronic amplifier was connected to a reference electrode placed on the skin flap. The amplifiers were in turn connected to a four-channel RM564 Tektronic storage oscilloscope. Unit activity was then photographed from the oscilloscope face using a Grass camera. In some experiments unit activity was used to activate a Schmitt Trigger (ST) which could be adjusted so as to be triggered reliably by units of amplitude above the noise level. This was continuously monitored by switching one of the oscilloscope channels to the output of the ST so that coincidence of the ST pulse and unit spike could be observed. Pulses from the ST were then fed to the input of a Mnemotron CAT 400A appropriately modified so that it could be used to compute poststimulus time histo-

grams. In this mode a synchronizing pulse from a stimulator starts the CAT to open its 400 memory gates one after the other at a selected rate; pulses being added within each gate while it is open. In this way it is possible to repeat the stimulus several times and obtain a cumulative count of how many times the unit fired during any interval after the stimulus.

Measurement of Directional Sensitivity. A luminous disc (20 ft-c) of adjustable diameter was moved by the control mechanism of an XY plotter. The experimental apparatus is schematized in Fig. 1. The XY plotter is in essence a machine consisting of two differential amplifiers, two servo motors and two servo control potentiometers, each one of which controls one of the two coordinates that define the position of a point on a plane. It is, therefore, possible by feeding appropriate electrical functions to the X and Y servo amplifiers to move a point on the display in any way one wants. In this study only horizontal and vertical scanning movements were used. This was achieved by applying a triangular wave to the X servo amplifier for horizontal scanning or to the Y servo amplifier for vertical scanning. The triangular wave was obtained from the A and B pins of the analog output of a Mnemotron CAT 400A. In this way every time the CAT receives a triggering pulse from the recycle pulse generator, a circuit in it is activated that opens the 400 memory gates which the machine has, starting from 1 and going to 400 with a speed which can be determined by a front panel switch and that can be varied from 0.62 to 32 sec. (Different speeds can be obtained by advancing the gates with pulses applied to the gate advance connection in the back of the CAT.) Each gate has its correspondent analog voltage along the slope of the triangular wave coming from pins A and B. This means that by using this output to operate the XY display a one-to-one correlation between memory gates and spatial positions on the display is achieved without further effort. In several experiments an artificial pupil was used. The background level of illumination was kept constant at 0.05 ft-c.

Light Flux Detection. In the same fashion as described above, the X analog output of the CAT was fed to the plus input of a differential amplifier (P65 Philbrick), which output was in turn made to control an electrically regulated power supply (855B Harrison Laboratories) connected to a light bulb. In these experiments the CAT gates were advanced every 8 sec with an external pulse. An I.R.C. B2m photocell was connected between the minus input of the amplifier and ground in such a way that the light bulb operated by the power supply and the photocell would form

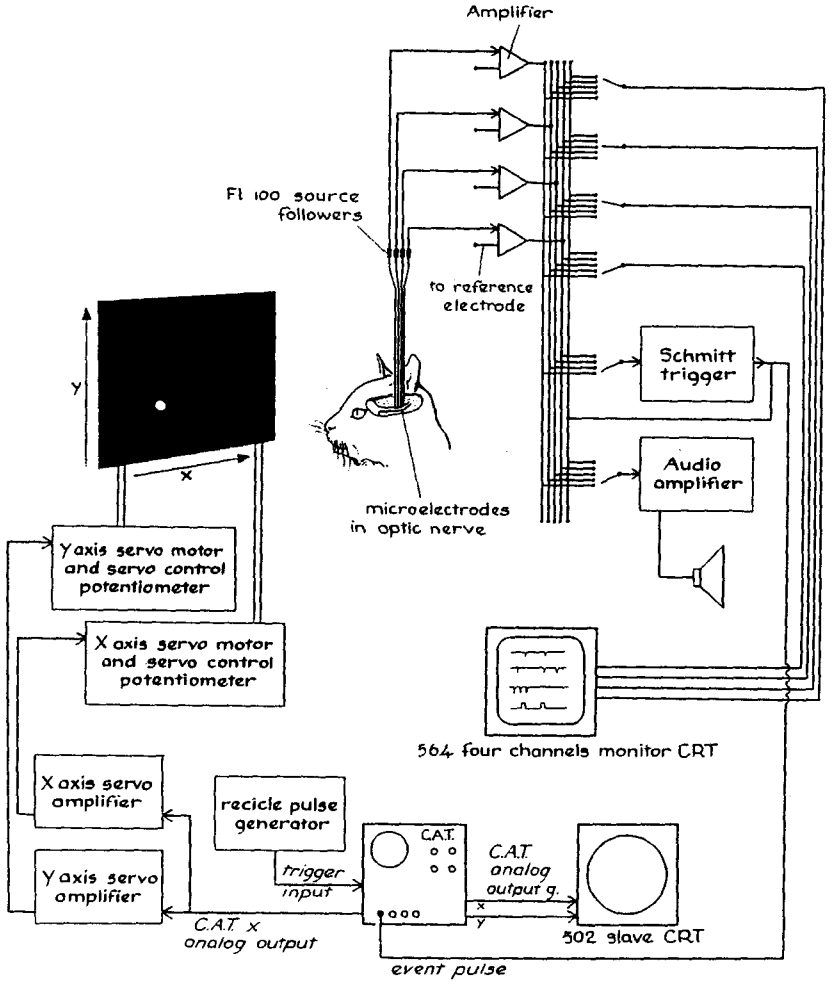

FIG. 1. Flow diagram of stimulating and recording setup.

a negative feedback loop. With this arrangement, and if the photocell is operated in the linear portion of its characteristic, the radiated power from the bulb is a linear function of the voltage applied to the input of the amplifier. The photocell was positioned on a screen illuminated by the bulb, the screen being 50 cm from the cat's eyes.

Mapping of Visual Receptive Fields: Visual receptive fields were first located by moving a wand with a small light bulb attached to the end in

front of the cat's eyes and then mapped in the same way described for the directional sensitivity measurements. Shock and click at the frequency of 10 per sec, were applied continuously when testing for their effects on visual receptive field organization.

The location of the electrode tips were determined in three ways: first, stereotaxically; second by adjusting the time constant of the amplifiers so that the optic nerve evoked responses to a flash could be detected, moreover a characteristic swish sound could at times be detected if the audio monitor volume control was turned very high; finally, histological verification of electrode tracts and holes made by passing 5 μamp for 5 sec was obtained.

Results

Efferent Units. The isolation and identification of single fibers in the optic nerve that would respond to auditory and somatic stimuli proved to be difficult. This contrasts with the relative ease with which efferent responses to auditory (A) and somatic (S) stimuli were recorded with gross chronically implanted electrodes, in the awake animal. The importance of comfort and "interest" on the part of the animal were previously emphasized; these conditions are not easily met in the acute preparation. It is of paramount importance that all incisions and pressure points be properly anesthetized and the over-all conditions of the animal optimal. To this end the long-acting local anesthetics already mentioned were used and excessively long experiments avoided.

Recordings were taken from 300 fibers in the optic nerve; of these fibers, 29 were identified as efferent. These fibers were selectively activated by click or shock or both. Figure 2 shows one such fiber that was activated by click and not by flash or shock. The firing pattern of these fibers was often unstable but usually the position of the first spike was regular enough to enable identification of the beginning of the discharge. Figure 3 shows another such unit activated by both click and shock. Records of unit activity to auditory stimulation were not always as clearcut as in Figs. 2 and 3. Most of the time a burst of spikes barely above noise level, either by itself or accompanied by a slow wave was observed after click or shock presentation. Only some of the efferent units studied had spontaneous background activity; this was not modified reliably by flash.

Afferent Units. A number of units with properties that have not yet been described for the cat's retina were identified during this and the following study (35). They will be briefly described here.

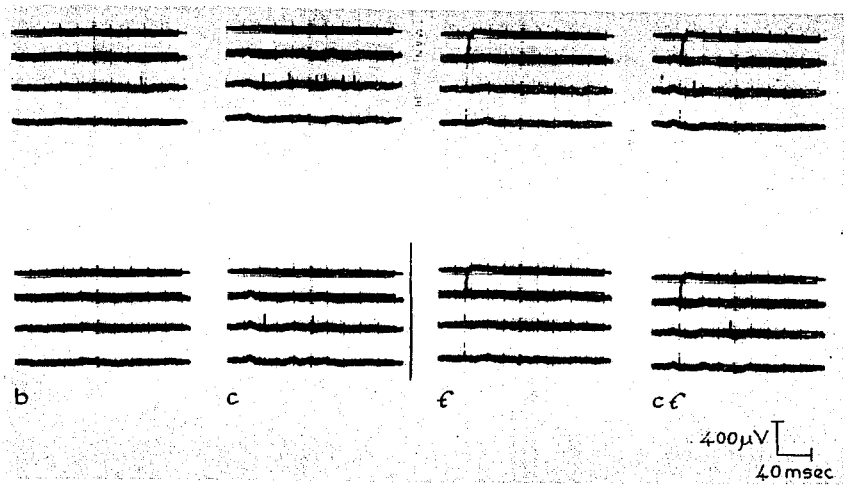

FIG. 2. The four traces of the oscilloscope from top to bottom represent: a photocell monitoring the flash, microelectrodes 2, 3, and 4. Microelectrode 3 is recording from an optic nerve fiber which is selectively activated by click; b indicates background activity, c click evoked response, f the flash evoked response, and cf the click-flash response. The click is presented at the beginning of the sweep.

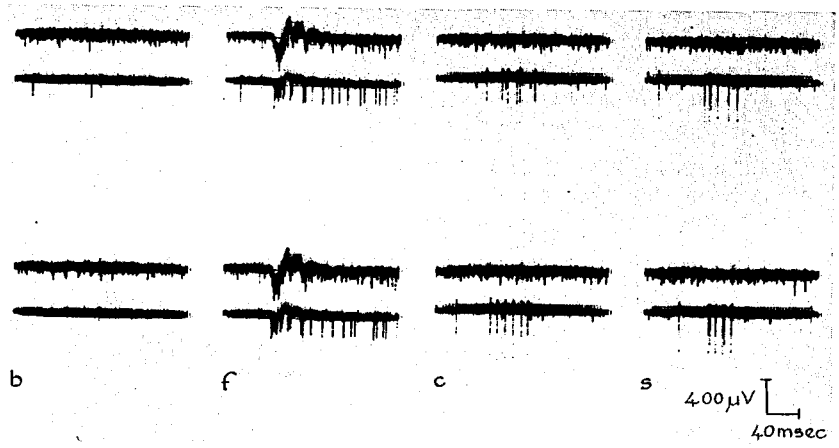

FIG. 3. In this series of records the second trace of the oscilloscope shows two units: a small unit in f is selectively activated by the flash; in c and s a larger unit is fired with a delay of 60 msec by the click and the shock.

Effect of Background Illumination. The firing level of the great majority of units we recorded from in the optic nerve was not affected by the absolute level of illumination (Fig. 4A). This is congruent with the description reported by Barlow and Levick (6). A few units, however, proved to be sensitive to the absolute level of illumination of the screen.

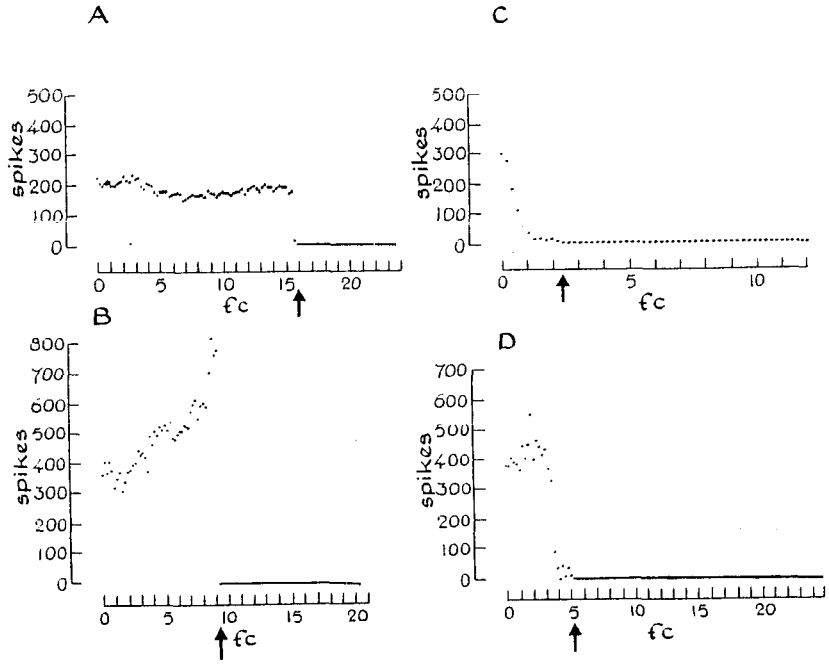

FIG. 4. Four optic nerve units exhibiting different response patterns to background illumination are shown in this picture. In A the number of times the unit fired in a 4-sec period is displayed on the ordinate; on the abscissa the level of screen illumination is expressed in ft-c. The firing rate of this unit remained practically unchanged from 0 to 15 ft-c. The arrow indicates the level of illumination at which analysis was stopped. In C and D the activity of two units is displayed which turns off when a 1-ft-c and 4-ft-c level is reached, respectively. In B a unit is shown whose activity increases proportionally with the level of illumination.

The units identified belonged to one of two categories. In the first the firing level of the unit remained unchanged until a certain level of illumination was reached, at which point the unit abruptly turned off. In Fig. 4C and D records from two units of this kind are shown; the unit in C was turned off by a very low level of illumination; the unit in D

was turned off only when the level of illumination reached 4 ft-c. In the second category the firing level of the units increased proportionally to the light level (Fig. 4B).

Directional Sensitivity. We noticed, while trying to locate receptive fields with the wand, that with some fields certain movements elicited brisker responses than others. We therefore mapped these fields with the spot of light moving in various directions. Figure 5 shows such a unit;

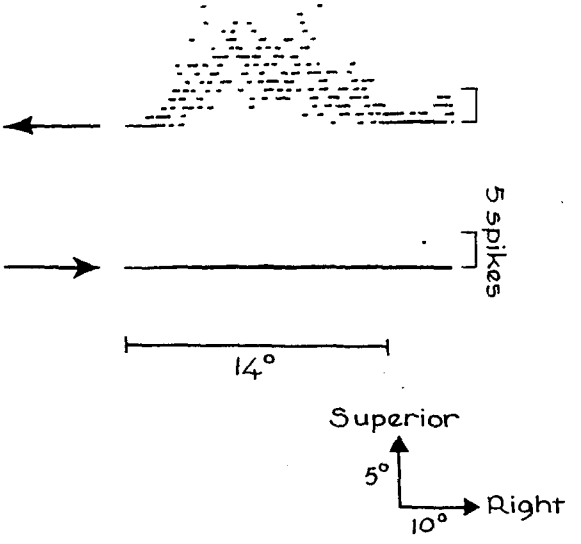

FIG. 5. Response histograms of an optic nerve fiber that fired only when the image moved from right to left. The diameter of the disc was 0.5° and the speed of motion 18° per sec; arrows on the left of the histograms indicate direction of movement. Each histogram represents the sum of ten scans. Arrows on lower right hand of figure indicate approximate position of the receptive field with respect to the visual axis.

this unit did not fire when the image moved from left to right, whereas it fired vigorously for movement in the reverse direction.[2]

Changes in Afferent Unit Activity Induced by Auditory and Somatic

[2] Direction sensitivity had been reported in the rabbit (4), pigeon (23) and frog (22) retina, and in the higher centers of the frog, rabbit, cat and monkey system (3, 15, 19, 20, 32). The lack of a prior report of this type of sensitivity in the retina of cat (10) is most likely due to the anesthesia used by these investigators or the different type of preparation used. Similar considerations might account for the lack of reports concerning flux detectors.

Stimulation. A variety of effects on afferent activity in the optic nerve was produced by clicks and shocks. These effects consisted of changes in background firing, in the firing pattern induced by flash, and in what we called "ordering" and "anticipatory" effects.

Background firing was increased by shock in twelve units and decreased in eighteen. Click increased background in eighteen units and decreased it in seventeen. The amount of change ranged from minimal to several times the baseline amount. The time course of the change induced by each individual click was not examined in detail but was very long lasting, so that at the frequency of stimulation used there was probably overlapping of effects.

Changes in Flash Produced Firing Patterns. The stability that most optic nerve units exhibit when responding to a flash of light makes the changes observed when the flash was preceded by a click or a shock striking and clear-cut. In Fig. 6 an example of such a unit can be seen: The background activity (b) is augmented 91% by the click (c) and the initial off period goes from 80 to 120 msec when the flash (f) is preceded by a click (cf.). Figure 7 shows two other units recorded simultaneously

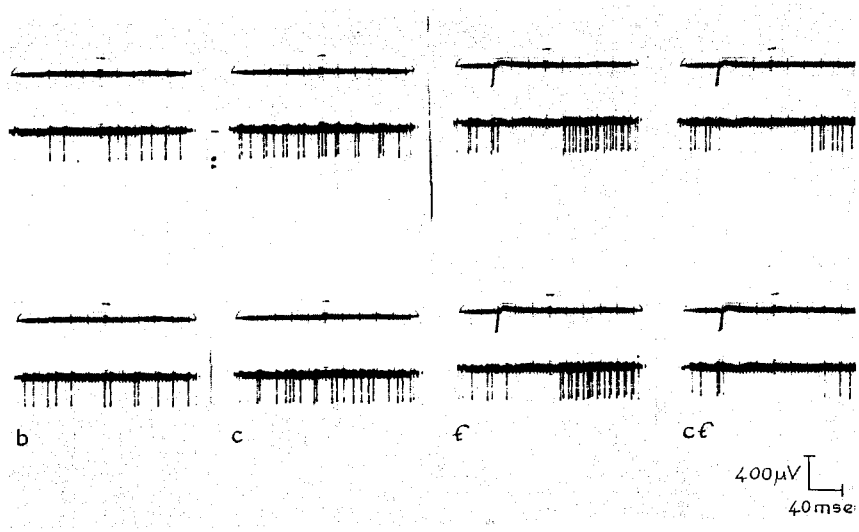

FIG. 6. In column b the background activity of a single optic nerve fiber is displayed in each record trace of the oscilloscope, in the first trace a photocell marker in c a click was presented at the beginning of the sweep; in f a flash, in cf click and flash at 40 msec interval (see text).

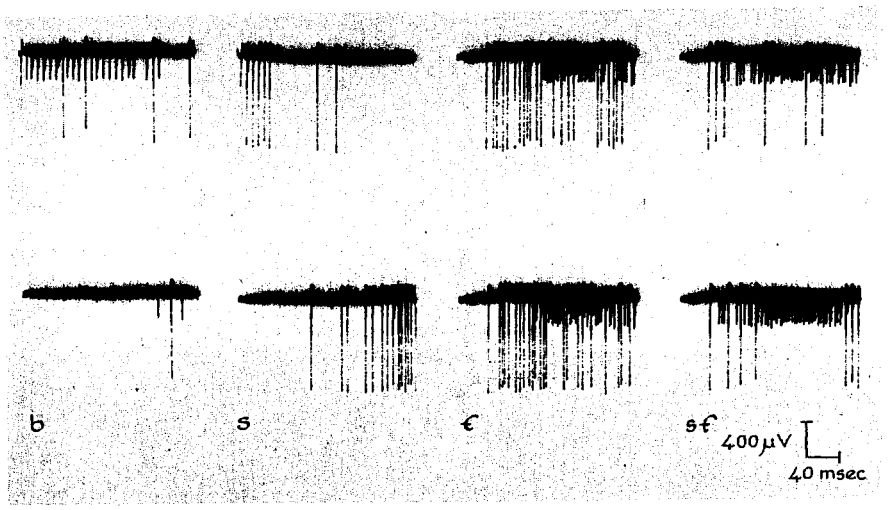

FIG. 7. In this experiment the microelectrode was detecting activity from two fibers, in b background, in s shock, in f flash, in sf shock and flash at 10-msec interval. Note the opposite effect the shock is producing on the two units.

from the same microelectrode; the background activity recorded in b is decreased for the small unit and increased for the large unit by the shock (s); the flash alone was given in f. When the shock precedes the flash, as can be seen in sf, delays and firing pattern were remarkably changed. There is a dramatic decrease in the number of spikes from the large unit and a 40-msec decrease in the latency of the small unit; moreover, a secondary off period appears for the large unit. Other units showed smaller but reliable changes when the flashes were preceded by clicks. Similar effects were obtained when shock was used as the preceding stimulus. The total number of units thus modified was twenty-three.

A number of units were analyzed using the post stimulus time histogram technique. With this method it is possible to add up the activity produced by a number of flashes presented with and without clicks; this magnifies the changes and reduces the effects of variability allowing a quantitative analysis of units, which show a highly irregular background or have an unstable firing pattern (Fig. 8).

Anticipation. This effect occurred upon discontinuing the flash after a long series of flashes: For a few seconds some units reorganize their background activity so that it appears as if the flash were still being presented.

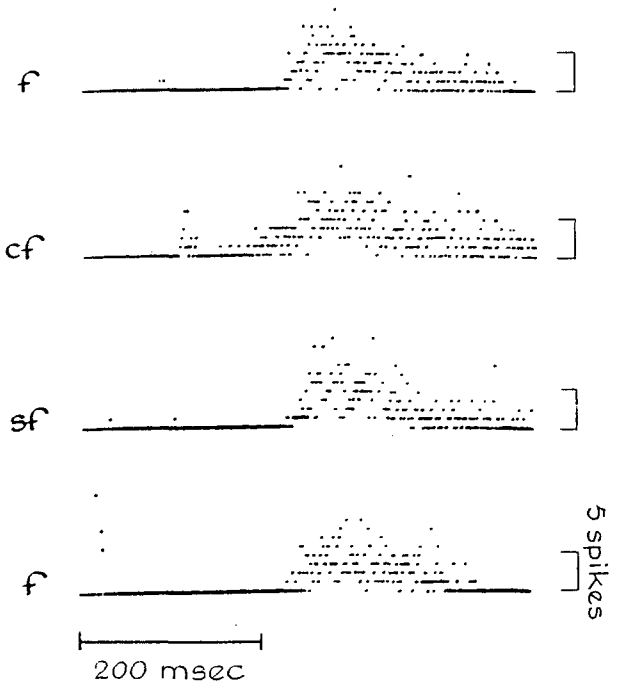

FIG. 8. Poststimulus time histogram of a unit to flash (f), click-flash (cf), shock-flash (sf) and flash (f) stimulation. For each histogram the stimuli were repeated five times. This unit firing pattern was altered by click but not by shock.

Ordering Effect. Several units which did not show the anticipation effect exhibited what we called the "ordering effect." In Fig. 9C when the flash is discontinued and the click presented, the spontaneous background of the unit which without stimuli is seemingly random, becomes organized in such a way that the activity after the click resembled the activity that would normally be produced by the flash. While this effect disappears rather quickly and not every click produced it, it is nevertheless rather striking, especially when heard from a loudspeaker.

Discussion

The identification of single fibers selectively activated by auditory or somatic stimulation proved to be long and tedious as compared with previous experiments performed with gross electrodes in the intact animal (33). On the other hand, the interpretation of the results once obtained is very straightforward. There can be very little doubt that these units are efferent,

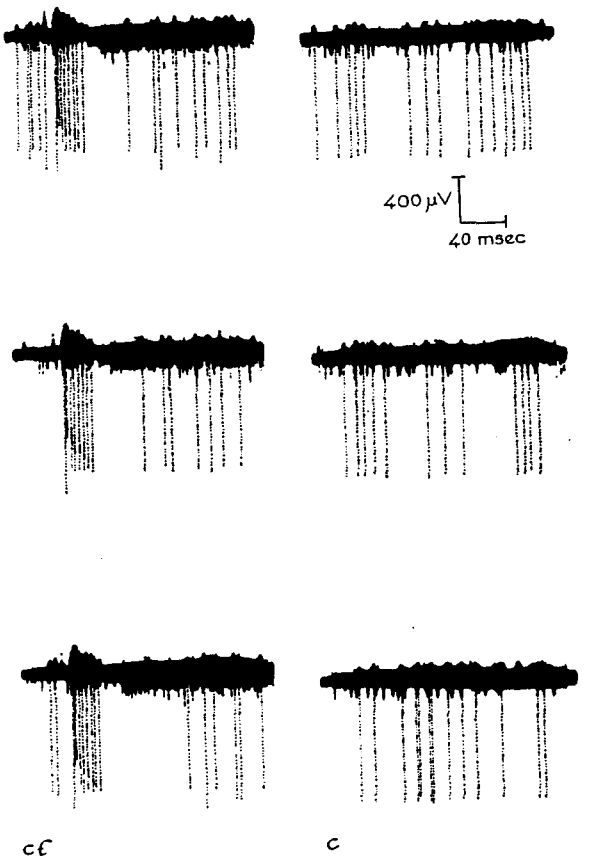

FIG. 9. Column cf from top to bottom shows the three last stimuli in a long series of click-flashes; column c shows three records taken with click only immediately after discontinuing the flash. The off period that is present when the flash is given continues to appear in the first and second click. The fiber fires randomly to the third click.

both on the basis of previous work (33) and because of the fact that they could not be activated by light. The same exacting precautions taken in the previously performed experiments were used in this study (33). Further, the dramatic changes produced in afferent units by click and shock stimulation are additional and powerful indirect evidence of efferent control of retinal activity. The small amplitude of the spikes recorded in most of the efferent units is a probable index of their small size. No precise ratio be-

tween afferent and efferent units can be given; 300 units being a small sample of the total population of fibers in the optic nerve. What is relevant is that efferent activity has been identified and measured at the unit level in the cat's optic nerve.

Such evidence of "centrifugal" activity at the retinal level has also been shown to be present in the rabbit by Dodt (12) and in the *Cynamolgus* monkey by Ogden and Brown (28). While these findings mirror the anatomical data (11, 13, 21, 24, 29, 31, 36) the presence of efferent fibers in the cat and in the optic nerve had remained still unproven. Moreover, the technique used in the other studies, i.e., electrical stimulation of the optic nerve or tract is open to a number of objections such as the possibility that the activity recorded was produced antidromically. Some of these objections are mentioned by the authors themselves (e.g., 12, 14). Auditory and somatic stimulation were used in the present study to overcome these difficulties of interpretation.

The same considerations apply to the changes produced in afferent units. Granit (14) had previously shown that afferent unit activity could be changed by electrical stimulation of the optic tectum; antidromic stimulation of afferent fiber could have been responsible for this change. By contrast, in the present experiments the stimuli responsible for the change in afferent unit activity were presented to the animal in a "physiological" fashion—namely, through the ear and skin. Thus, the fact that the changes are induced via efferents is clearly established.

The most common change observed is an increase in background activity accompanied by a lengthening of the initial off period to a flash or a decrease in background accompanied by a shortening of the initial off period. These seemingly paradoxical effects are the most reliably produced. Less reliable but striking are the "ordering" and "anticipation" effects. These two effects are probably the same phenomenon produced by different stimuli acting efferently on the retina: click for ordering and repetition rate for anticipation.

These results lead to the inescapable conclusion that when the animal hears a sound or receives tactile stimulation there is a substantial reorganization of the visual input. However, the type of analysis used here is still far too crude to indicate the nature of this reorganization. It was therefore deemed necessary to study the receptive field organization of the retina and the changes produced in this organization by auditory and somatic stimuli. To this end the following study (35) was undertaken.

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