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Centrifugal Optic Nerve Responses Evoked by Auditory and Somatic Stimulation

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The evidence for the efferent control of receptor events has recently been repeatedly challenged. The present experiments were undertaken to provide a simple demonstration of the existence of such a mechanism. Clicks were presented to unanesthetized cats and bipolar recordings made of potential changes evoked in the optic nerve and tract with implants of small (300 μ spaced about 0.2 mm) electrode wires. Click initiated optic nerve responses of 10 60 μv amplitude were obtained in fourteen cats at a latency of 20 msec. These responses were unaffected by atropinization or by curarization; they showed amplitude decrement upon repeated presentations and were unobtainable when the animal was restless. They were abolished by bilateral section of the optic tracts central to the implant sites. Similar optic nerve responses could be initiated by tactile stimulation. Also, silent flash produced recordable responses in the eighth cranial nerve. Finally, parametric click-flash interaction effects were observed to differentially affect different fibers in the optic nerve and to alter the B wave of the ERG.

Introduction

A considerable amount of research (1, 7, 8, 11, 12, 15, 16, 19, 20–23, 28, 29) has been done on the problem of efferent control of receptor functions since Lexell (24) demonstrated that muscle-spindle activity is dependent not only on the amount of tension applied, but also on the firing rate of the gamma neurons that innervate them, and Granit and Kaada (17) showed that the gamma efferents are, in turn, influenced by the brain-stem reticular formation and other central structures.

Despite this, the evidence for an efferent system to the retina is still controversial. As early as 1889 Von Monakow (36) and later in 1894 Ramón y Cajal (32, 34) had found fibers in the vertebrate retina that terminate in the seventh layer around the amacrine cells. He suggested that these are centrifugal fibers and Dogiel (13) traced them back to the optic

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papilla. This finding has been recently confirmed by Cragg (11). However, no one has yet demonstrated such efferents in the optic nerve (5, 6, 30, 37).

Other authors have specifically claimed that there are no efferent fibers to the retina (7). Yet indirect evidence for the existence of efferent control over retinal activity is available (4). Motokawa (28) in 1953 found that stimulation of the optic nerve differentially changes the electrical activity of the retina to flashes of different wavelength. Dodt (12) in 1955 found that there is a late "antidromic" spike in the retina which comes after the true antidromic spike initiated by stimulation of the optic tract. The late spike is frequency sensitive and disappears temporarily during moderate light adaptation and it is suppressed by myanesine. This suggests that it is post-synaptically produced. Granit (16) demonstrated that stimulation of the mid-brain tegmentum has an augmenting effect on the firing rate of active ganglion cells in the retina though at times inhibitory effects are obtained. Suggestive as this evidence may be, there is no conclusive direct demonstration in the literature of efferent activity in the optic nerve elicited by a "physiological stimulus."

That efferent activity directly influences afferents in the auditory nerve (15, 34) has also not gone unchallenged (18). The suggestion has been made and supported by evidence, that these influences are the result not of action on the receptor cells themselves nor on the neural elements in the cochlea, but that they are due to changes in tension of the inner ear muscles. For this reason, eye movements, pupillary changes and the like have been advanced as explanations of the observed changes in afferent activity in the optic nerve.

Efferent control of sensory systems is of considerable theoretical significance (25, 27, 31). The present experiments were thus undertaken to determine whether efferent activity could be elicited in the optic nerve or in other sensory nerves by physiological stimuli, and to define some of the functional properties of such activity.

Electrodes were chronically implanted in the optic nerve of cats and indeed such efferent responses were evoked by auditory and tactile stimuli. Further, evidence of centrifugal activity in other sensory systems was sought in this fashion. Finally, auditory click effects on the eletcroretinogram were demonstrated in order to test whether these efferent mechanisms play some physiological role.

Methods and Materials

General Procedures. Fourteen cats were used. Electrodes were chronically implanted bilaterally with the aid of a stereotaxic instrument under Nem-

butal anesthesia. Aseptic precautions were taken. Bipolar and quadripolar electrodes were aimed at the intracranial end of the optic foramen. The final positioning of the recording electrodes were based on observation of the optic nerve responses to light flash stimulation. Differential recording between the electrode tips as they were lowered allowed highly accurate placements within the optic nerve. Histological or surgical verification of the placement was also obtained (Fig. 1).

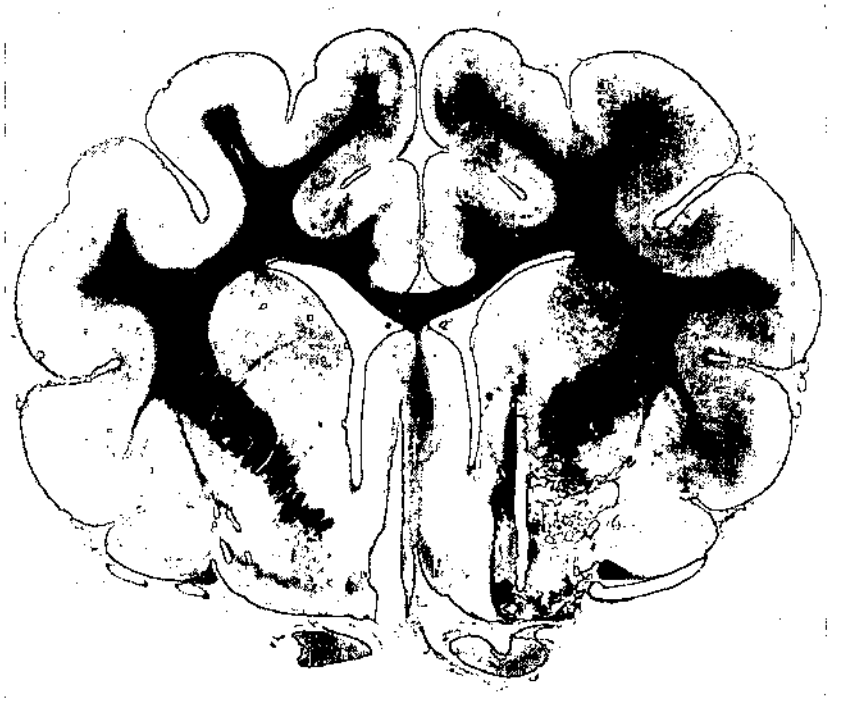

FIG. 1. Cross section of electrode implantation (stereotaxic coordinate AP16) site in optic nerve.

The electrodes consisted of either two or four enamelled nichrome wires (300 μ in diameter) insulated to the tips and kept together by an insulating varnish. The tips were formed after the varnish had dried by simply cutting the wires perpendicularly to their length. The separation between the tips was therefore only that which was afforded by the enamel coating (Fig. 2).

Electrically, the electrodes behaved as if the tip separation was 200 μ. This measurement was obtained by placing the electrode pair in a solution

to which an alternating electric field of a known gradient was applied and by measuring the difference in potential detected by the electrodes. All electrodes were checked with an ohmmeter to verify that there was no short-circuiting of the tips, and, with a saline loop along the stem to insure that no breaking of the enamel or of the insulating varnish was present. With this very small tip separation the evoked responses recorded from the optic nerve or other subcortical brain structure are smaller than those that can be obtained with greater tip spacings; on the other hand, spatial resolution is very great as can be seen from Fig. 3.

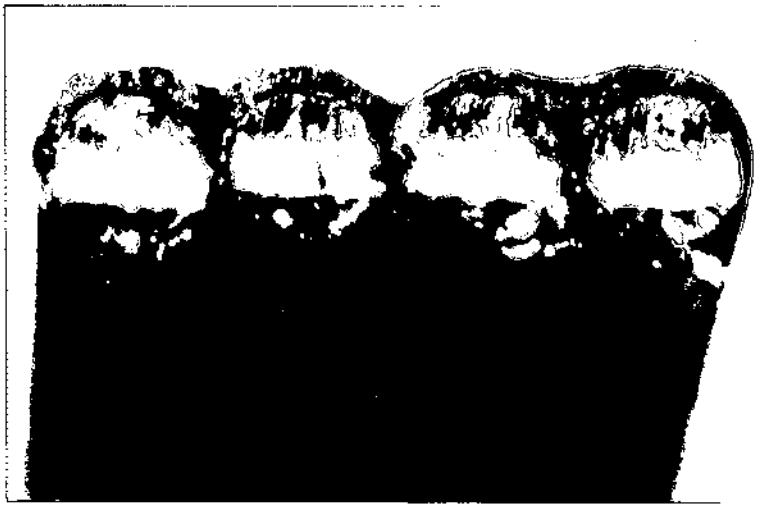

FIG. 2. A view of electrode tips 100 times magnified. This is an array of four electrodes as used in some of the experiments. More usually only two wires were inserted at any time.

After positioning, the electrodes were secured to the skull with Nuweld dental cement and then threaded through an 8 S. M. Cinch-Jones subminiature socket which was also cemented to the skull.

Experiments with Flaxedil. A number of experiments were performed while the animals were under the action of Flaxedil (gallamine triethiodide). During a brief ether anesthesia the pharynx of the cat was sprayed with Dorsocaine (benoxinate hydrochloride) and a soft canula moistened with the same local anesthetic was then inserted into the trachea through the mouth. Flaxedil was given intravenously in a single dose of 20 mg/kg. Homatropine, Cyclogyl (cyclopentolate chloride) and Dorsocaine were

instilled into the eye. The animal was then put in a comfortable position on a foam-rubber pad and allowed 30 min to recoved from the ether anesthesia. The respiration level was kept as close as possible to the one that was observed prior to the injection of Flaxedil. For the recording of the electroretinogram (ERG) a small silver-silver chloride electrode was placed on the cornea. A reference electrode was inserted under the skin on the nasion. Except for an amplifier time constant of 2 seconds, recording technique was as described in the Experimental Situation.

Special Surgical Procedure. Four cats were given bilateral, and two cats a unilateral optic tract section. The approach was made through a myeloplastic temporal craniotomy, the middle cerebral artery exposed and followed down to the circle of Willis. Exposure was facilitated by temporary packing with cotton of the space between the brain and the base of the skull. When the tract was properly visualized it could easily be severed with suction and a malleable brain retractor. The previously implanted electrode tips in the optic nerve, and the optic chiasma were routinely identified. After the tract section, closure was effected with interrupted silk technique. Whenever the bilateral procedure was carried out, the second side was operated upon immediately the first side was completed. The only complication encountered was bleeding from some of the smaller tributaries of the circle of Willis. These were controlled by gentle pressure and waiting.

Experimental Situation. A period of 2–6 weeks was allowed for recovery after surgery. All experiments were carried out in a shielded box 60 cm high, 40 cm wide, and 90 cm long. The entire box was made of aluminum except for a side wall consisting of a one-way plastic mirror and for the front end which was made of sanded Plexiglas. Through this translucent screen, light stimuli could be given to the animal. A Grass PS-2 photostimulator was used. A rectangular pulse of 1-msec duration taken from the output of a Grass S-4E stimulator was led to a loud speaker that was placed about 50 cm from the animal. The voltage of the pulse was adjusted so as to produce a sound intensity of about 60 db as referred to a sound pressure of 0.0002 dynes/cm^2. Light flashes and clicks were given at a frequency of 0.5/sec. Microdot wire cables were used to connect the animal to the amplifiers of a Grass EEG machine; the output from the amplifiers was then averaged with a Mnemotron CAT 400A and photographed. Some records were made by displaying repetitive traces on a Tektronix 502 oscilloscope and photographing them by superimposition on Polaroid film. A Goodman Vn7 vibration generator was used for somatic stimulation. Homatropine and Cyclogyl were used routinely on all cats.

Results

Optic Nerve Responses Evoked by Auditory Clicks. Figure 3a shows a record of optic nerve activity to light flashes of moderate intensity, the number of responses averaged is ten. The upper two traces were each differentially recorded from one of the two pairs of electrodes that make up the electrode assembly shown in Fig. 1. This was located in the right optic nerve. The two lower traces of Fig. 3a were recorded with the same type of electrode placed in the left optic nerve.[2]

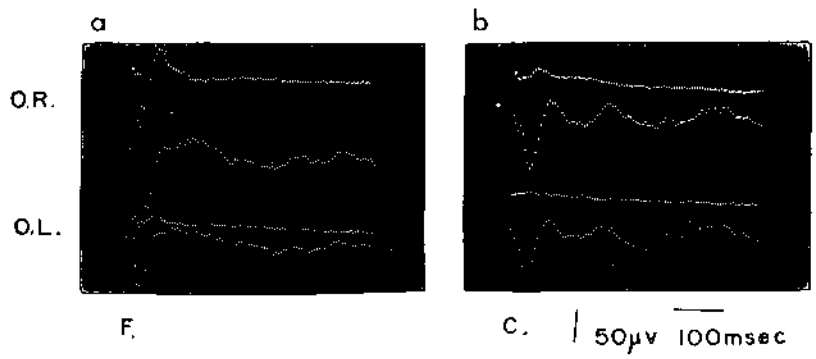

FIG. 3. Right and left optic nerve responses recorded with quadripolar electrodes. Figure 3a shows responses to flash (F); Fig. 3b to click stimulation (C). Note in b two top traces, that one electrode pair is detecting electrical activity to clicks while the other pair of the same electrode assembly shows very little.

Figure 3b shows optic nerve responses to click stimulation; there is very little activity in the top trace corresponding to the first electrode pair in the right optic nerve; this electrode pair had shown good responses to light stimulation; the second trace from the top shows a wave of about 60 μv in amplitude and 20-msec latency; this pair had also shown good responses to light stimuli. The two bottom traces of Fig. 3b belong to the two electrode pairs that were placed in the left optic nerve. The second pair shows also activity evoked by the clicks; amplitude and latency are of about the same

[2] There is a great difference in amplitude and wave form of these two traces: Even if the smaller of the two was due to nothing else but volume conduction from the elements that were active under the pair from which the bottom trace was recorded it is clear that the attenuation factor for a distance as small as the distance between the two electrode pairs is of the order of five times or better (two bottom traces in Fig. 3B). On this basis and because of the very small interelectrode distance it seems reasonable to assume that each electrode pair is recording activity from a very small population of fibers, no more than a few hundred.

value as those measured in the right optic nerve. The amplitude range of these responses in the experimental group was from 10 to 60 μv, and were not visibly affected by Homatropine, Cyclogyl and Flaxedil (Figs. 6, 9). Changes in background illumination had inconsistent effects, sometimes increasing, sometimes decreasing slightly the amplitude of the response. The best records were obtained when the animal was quietly attentive; an example of this shown on the left side of Fig. 4. Here five consecutive

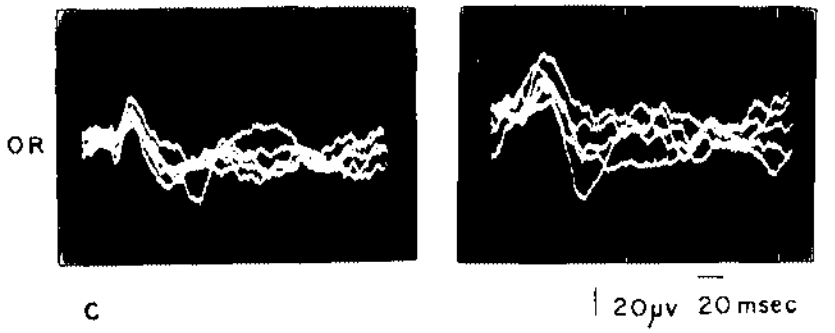

FIG. 4. Recording made with a bipolar electrode implanted in the optic nerve, of electrical responses to click stimulation (C). Whereas in all other figures the response has been accumulated on a Computer for Average Transients (CAT), this record was made directly from the oscilloscope face by superimposition on photographic film. The left record was made when the animal appeared to be "attending" while the right record was made with the animal "distracted."

responses to clicks were recorded while the animal was quiet and attentive, while on the right are shown five consecutive superimposed traces also to clicks obtained while the animal was restless. Irregularities of response or its absence occurred when the animals were drowsy or asleep.

Surgical section of the optic tracts central to the implanted electrodes permanently abolished optic nerve responses to the clicks while leaving the response to flash unimpaired (Fig. 5).

All animals were chronic preparations; of these, several cats were studied while under the action of Flaxedil (see Method) from which they recovered promptly and completely 2–3 hours after the first injection. A representative case is shown in Fig. 6. In this experiment clicks were presented continuously at the frequency of 0.5 per sec over a period of 2 hours; averages of fifty clicks each were recorded 60, 90, and 120 min after the control record. Click evoked responses are present in the optic nerve even in the Flaxedilized preparation. There is a slow decrement in the amplitude of the

responses so that at the end of 2 hours the response is reduced to about half of its original value. No return to the original amplitude of response could be obtained over the duration of the Flaxedil activity (about 3 hours), but the following day the record had resumed its typical initial appearance.

Optic Nerve Responses to Somatic Stimulation. Vitratory stimulation of the paw evokes optic nerve activity. These potentials correspond closely to the ones evoked by auditory stimulation. After a 20-msec latency a wave

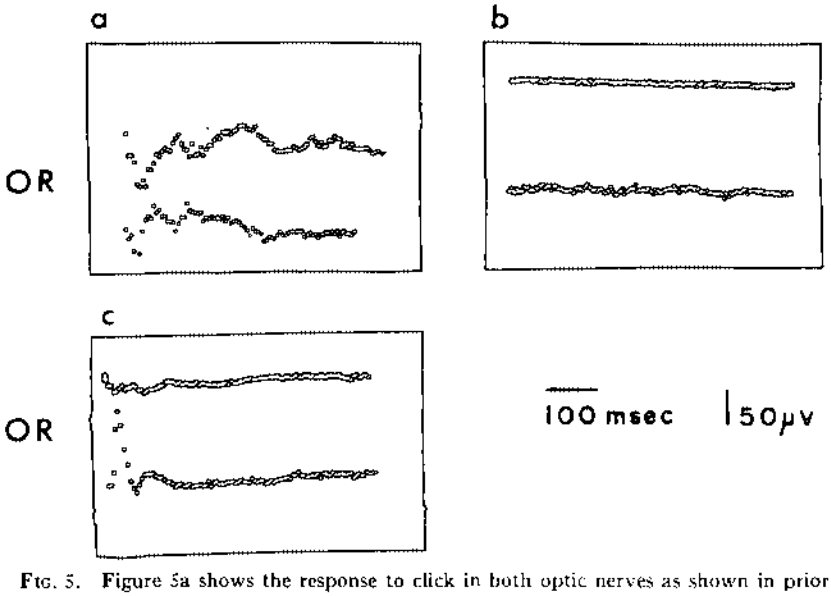

FIG. 5. Figure 5a shows the response to click in both optic nerves as shown in prior figures. Figure 5b shows the disappearance of this response after bilateral optic tract section. Figure 5c shows that optic nerve response to flashes can still be obtained.

lasting 50–60 msec, 10–50 μv in amplitude was detected. This wave was followed by slower waves of variable amplitude. Figure 7 shows an averaged response to fifty low-intensity vibratory stimuli applied to the right paw of the cat.

Auditory Nerve Responses to Light Flashes. The right bottom trace of Fig. 8 shows that auditory nerve responses are produced by light flashes. Since electronic flashes also produce a click the unit had been thoroughly sound shielded and an intense masking noise was used to minimize the possibility that these responses were artifactual. The latency of the response which is of the order of 30 msec suggests that the responses are, in fact, due to the light stimuli since responses from the same electrode to clicks had

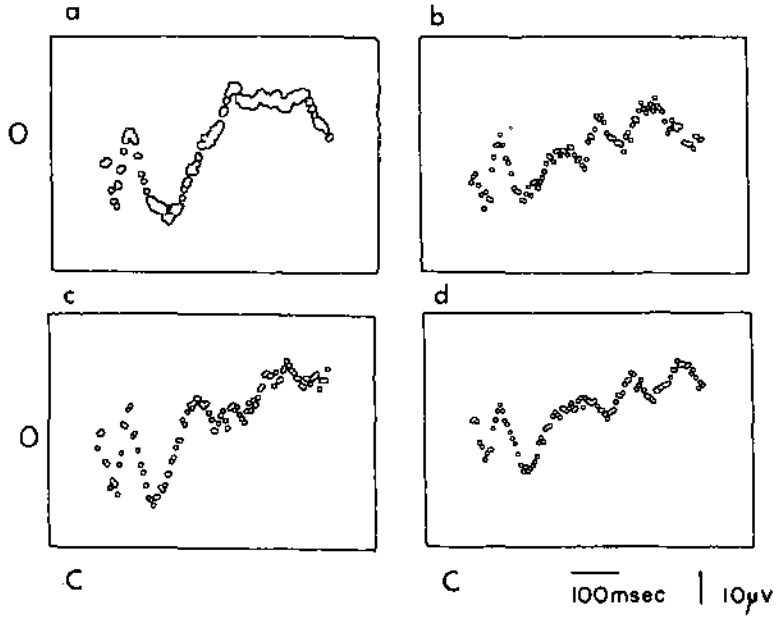

FIG. 6. These records were obtained during long term click stimulation at the rate of 1/sec; record a made at 0 time, record c at 30 min, record b at 1 hour, and record d at 2 hours. The preparation was curarized. Note that electrical response to clicks are still present in the optic nerve during curarization. A decrease in amplitude can also be observed to take place over the 2-hour period.

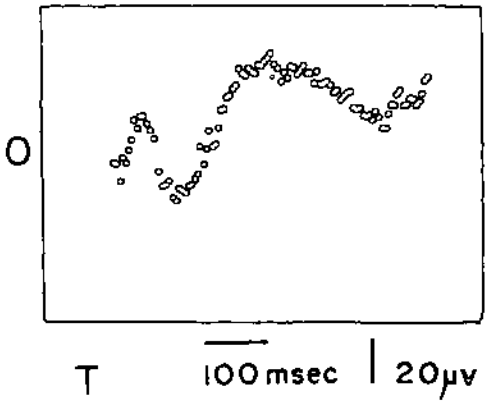

FIG. 7. Response in the optic nerve to tactile stimulation of the forepaw (T).

latencies of less than 5 msec. (The gating system of the averager makes time resolution dependent on the time base that is used.)

Olfactory Bulb Activity During Light Stimulation. Although anatomical evidence for the existence of efferent fibers to the olfactory bulb seems well documented no activity could be detected in the olfactory bulbs to sound or

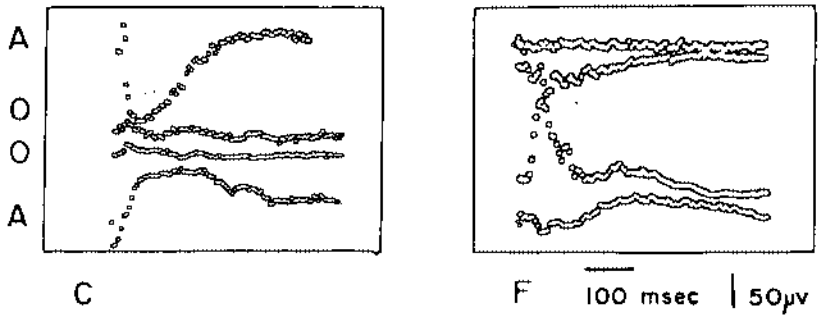

FIG. 8. Response in the optic (O) and auditory (A) nerves to clicks (C) and flashes (F) in an immobilized cat. Note the short latency of the click response in both auditory nerves as compared with the long latency of the electrical response produced by flashes in the same nerves.

light stimulation (Fig. 9). This may be due to the high amplitude of "spontaneous"—i.e., not time linked to the stimulus—electrical activity of the olfactory bulb.

Modification of ERG and of Photically Evoked Optic Nerve Activity. The ERG was used in an attempt to test the physiological efficacy of

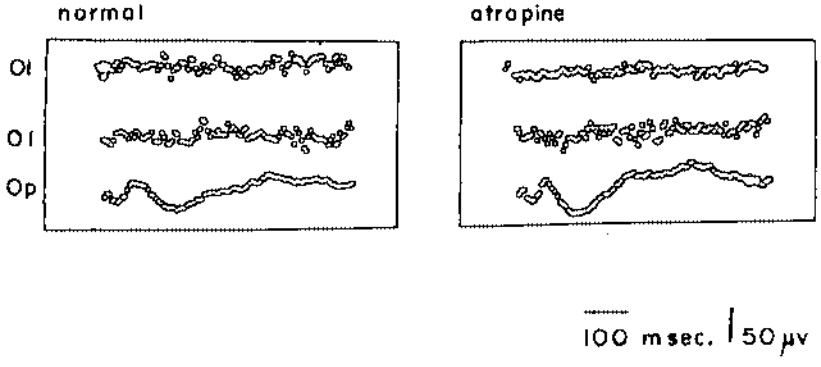

FIG. 9. Records made in the olfactory tracts (OL) and optic (OP) nerve to clicks in normal and atropinized subjects. No responses could be obtained from the olfactory tracts in these experiments.

efferent activity on the retina. Figure 10 shows records taken from an unanesthetized Flaxedilized and atropinized preparation. The top left record a, shows a control average of ten responses; records b, c and d show averages of ten responses to a flash of light of the same intensity as the control, but preceded by a click with an interval of 100, 200 and 300 msec. There is a progressive inhibition of the b-wave, while the c-wave seems unaffected. In e appears another control average, taken at the end of the series.

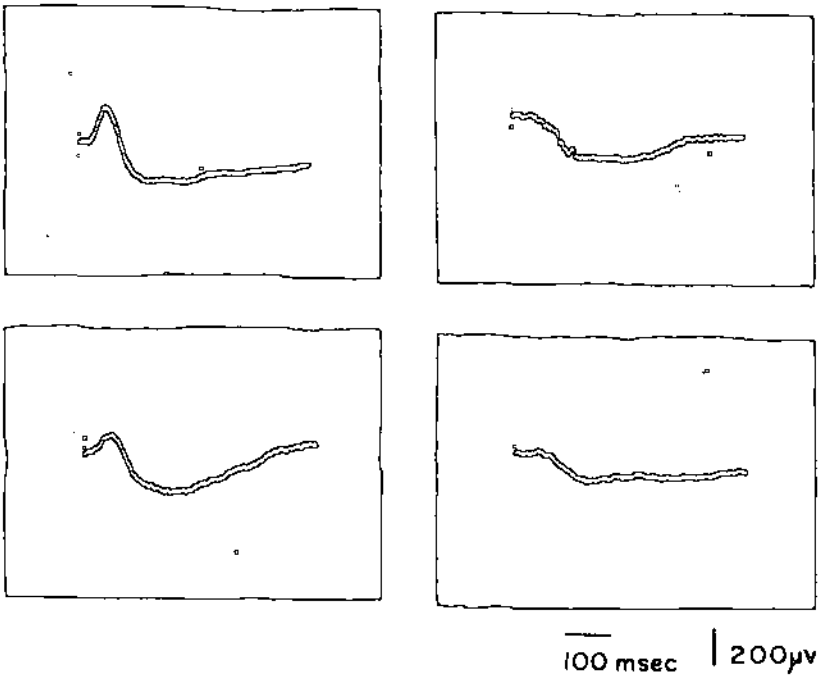

FIG. 10. Click-flash interaction effects on the electroretinogram in the curarized-atropinized preparation. In a, ERG to flash alone; b, c, and d, click flash at 100-msec, 200 msec, 300-msec interval; e, another control flash at the end of the series.

The effect of click-flash interactions on optic nerve activity was also studied. The top trace of Fig. 11a shows records from the two electrode pairs of a quadripolar assembly placed in the left optic nerve; the two bottom traces were recorded with the same type of electrodes from the right optic nerve after light stimulation; the four tracings of Fig. 10b show responses to light flashes when the light stimulus was preceded by a click at

an interval of 50 msec. All tracings are the average of fifty responses. Note that the first electrode pair in the right optic nerve (third tracing from the top) shows a reduced response to light stimulation when the flash was preceded by the click, and that a very small distance away, the second electrode pair (fourth tracing from the top) shows practically no change.

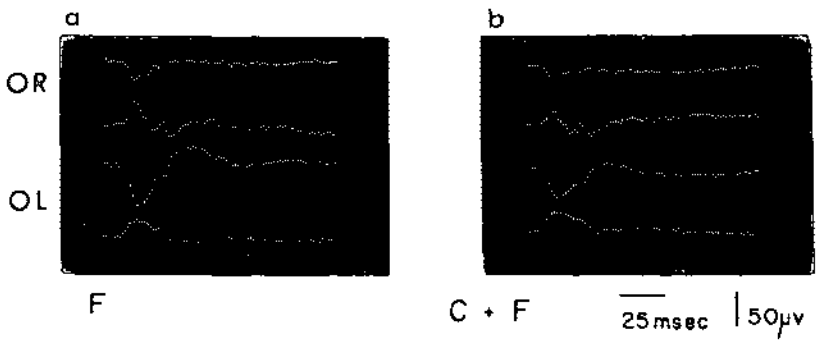

FIG. 11. Quadripolar recording of click–flash interactions as they affect the optic nerve response. Figure 11a shows the record obtained when flash alone is presented. Figure 11b records the click–flash interaction using a 50-msec interval. Note that while the electrical response to the flash recorded in the bottom trace is not affected by the preceding click, there is a clear-cut reduction in the amplitude of the response detected by the other pair of electrodes of the same assembly.

Discussion

This work can be divided into two parts: The first has to do with optic nerve responses to auditory and somatic stimulation. If it is shown that these responses are not artifactual, then an efferent system to the retina will have been convincingly demonstrated. The second part concerns changes induced in afferent activity when auditory stimuli precede the flash.

The Optic Nerve Responses. There are some features of these responses which might at first seem puzzling; in Fig. 3, for example, the amplitude of the click evoked response is of the same order as the flash evoked response. This is by no means always the case (Fig. 8), and it must be interpreted as an effect of the small interelectrode distance that was used. The electrodes are detecting the activity of the very few fibers between them and give no indication of the over-all activity of the optic nerve. No conclusion can therefore be drawn about relative numbers of afferent and efferent fibers in the optic nerve. The same reasoning explains why responses recorded from one pair of the quadripolar assembly may look entirely different from

responses recorded from the other pair which is only 300 μ away. These differences are in fact, an actual test of electrode selectivity and their existence the reason for using such electrodes at all, namely, to show that the records obtained are the result of activity of fibers in contact with the electrode tips and not of volume conduction from other structures.

The experiments were carried out in chronically implanted fully awake animals. The occasions for artifact were therefore considerable. We thought of the following and tried to control for them.

Pupillary Changes. The criticism has repeatedly been urged that whenever changes in afferent activity are observed they are due to changes in effectors associated with the receptor mechanism (18). In the present experiments, the subjects' eyes were routinely atropinized. Further, pupillary reflexes have a latency of about 200 msec—some 180 msec longer than the click responses evoked in the optic nerve in this experiment.

Ciliary Muscle Contraction. Here again, the latency of the responses (3) observed in these experiments is evidence against origin in ciliary muscle contraction. In addition, Homatropine and Cyclogyl were used, and the click evoked optic nerve responses were still present.

Volume Conduction from Neighboring Brain Tissue. As already emphasized (see footnote 2) the small interelectrode distance and their small size made the electrodes highly selective. The evidence from the reported series of experiments is that recordings at a distance simply did not happen.

Volume Conduction from Skeletal Muscle Activity. Aside from the facts of electrode selectivity, the use of Flaxedil excluded this possible source of artifact in these experiments.

Vascular changes in Optic and Retinal Vessels. The abruptness of the responses evoked and their short latency argue against this possible artifact. Further, the fact that the responses ceased after optic tract section central to the electrodes, places the origin of these responses central to the cut.

Eye Movement Responses to Clicks with the Resultant Shifts in Retinal Images. Such responses usually have latencies around 200 msec, (3) while the responses in these experiments appeared in the 20-msec range. Further, observation of the eyes and Flaxedil were used to rule out this possibility for artifact.

In summary, we think that the small electrode size, the atropinization of the eye and Flaxedilization of the animal, controlled for possible artifacts. Moreover, the disappearance of click evoked responses in the optic nerve

after resection of the optic tract clearly indicates that their original is central to the section.[3]

Similarly, efferent responses were sought in the auditory nerve and olfactory tract to light and sound stimulation, respectively. Long-latency responses were detected in the auditory nerve (30 msec); click induced responses in the auditory nerve have latencies of only 1 or 2 msec (33). In fact, Ades and Brookhart (2) have shown that the longest latency to click responses that can be found in the auditory system is about 13 msec in the secondary auditory area. This seems to indicate that the origin of this response cannot be attributed to an insufficient shielding and masking against clicks by the electrically produced flash. No click or flash induced activity could be detected in the olfactory tract.

Changes Induced in Afferent Activity. The second group of results deals with changes in click evoked responses in the optic nerve to repeated presentations, and with modification in optic nerve activity and in the ERG induced by a preceding click. Clicks were presented for periods of up to 2 hours to Flaxedilized preparations. The suggestion has been made (26) that efferent control of receptors and sensory transmission systems might be involved in "shifting attention" from one sensory stimulus to another and in "habituation"; if so, optic nerve responses to sound stimuli should show a decrement in amplitude with repeated presentations. Figure 6 shows that this is indeed the case.

However, the prolonged time course of the onset of the decrement and the failure to obtain a return to normal within the limits of the experimental situation made this result difficult to interpret.

The ERG changes by various agents are not new in the literature. Jacobson and Suzuki (22) in 1962 demonstrated that cutting the optic nerve changes the recovery cycle of the ERG in the sense that return to normal of the second response is faster. This was interpreted to indicate that an efferent system from brain to retina has been interfered with.

[3] A further possibility was considered, namely that these responses could be conceived in the same class of the dorsal root reflexes. This would imply that presynaptic inhibition (14) was at play in audiovisual interactions. While this interpretation would not detract from the general concept that afferent systems can be influenced by higher structures, it is very unlikely; dorsal root reflexes require an intimately common interneuron pool (9) which is not present in the visual and the auditory systems.

Since this work was completed Weingarten has been conducting microelectrode studies on the optic nerve. This work has just begun and only about twenty units recorded from. One of the twenty responded to click only; none of the units that were activated by flashes responded to click.

However, Brindley and Hamasaki (8) have contested that any changes in the ERG are produced by the cutting of the optic nerve. In our experiments, clicks produced changes of the b-wave of the ERG, with little or no change in the c-wave; these components of the ERG have been attributed to the inner nuclear layer of the retina, and to the pigment epithelium, respectively (10). Click induced modifications in the optic nerve responses to flashes were also found; these results were especially clear-cut because it was often possible to induce changes only in some of the electrode derivations. This selectivity demonstrates both that the observed change was not due to a spontaneous shift of the response and that the efferent activity exerts itself in a discrete fashion rather than as a common facilitatory or inhibitory influence. This result agrees with Granit's finding on single units (16).

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